23

I

QUAIN'S ANATOMY

THE HEART

Quain, Jones

QUAIN'S

ELEMENTS OF ANATOMY

ELEVENTH EDITION

EDITORS

THOMAS HASTIE BRYCE, M.A., M.D., F.R.S.
PROFESSOR OF ANATOMY IN THE UNIVERSITY OF GLASGOW

THOMAS WALMSLEY, M.D.
PROFESSOR OF ANATOMY, QUEEN'S UNIVERSITY OF BELFAST

IN FOUR VOLUMES

VOL. IV. PART III.

THE HEART

BY THOMAS WALMSLEY

WITH FOUR COLOURED FIGURES AND OTHER ILLUSTRATIONS

LONGMANS, GREEN, AND CO.
LONDON : NEW YORK : TORONTO
1929

Made in Great Britain

PREFACE

THE present volume is a memoir on the human heart. It was originally intended that Part III. of Volume IV. of the present edition of this work should embrace the whole subject of Angiology. On mature consideration, however, it was decided that there was nothing so novel in the descriptive accounts of the arteries and veins as to justify the issue of Part III. as designed, in view of the necessarily limited demand for a book on this scale. It seemed different as regards the heart. Much new work has been done on the anatomy of the heart, and in certain of its aspects the subject is of importance to the physician as well as to the anatomist. It was determined, therefore, that the chapter on the heart, which was undertaken by Professor Walmsley, should be issued in somewhat altered form as an independent monograph, and that the remaining sections should be dropped. The section on the lymphatics, which was written by Professor D. M. Blair, will appear elsewhere.

This volume will therefore bring the present edition to a close, and it is the hope of the undersigned that it will prove of value to the clinician as well as to the anatomist, both for the information made available for reference, and for the accounts furnished by the author of the genetic system, the vascular arrangements, and other important topics. It is also hoped that the bibliography will be useful to workers on the subject.

Cordial acknowledgments are due to Miss M. E. Rea for many excellent drawings, for the secretarial assistance which greatly facilitated the production of the work, and for the preparation of the Index.

THOMAS H. BRYCE.

CONTENTS

THE HEART

THE STRUCTURE OF THE HEART

INTRODUCTION

THE function of the **circulatory system** is to distribute the blood to the individual parts of the body and there to bring it into such relation with the elements of the parts that they may gain from it the substances necessary for their function, especially the required supply of oxygen, and discharge into it the products of their activity. The blood remains, however, in its whole course from the **heart** to the tissues of the body and from the tissues back to the heart within a closed system of **vessels**, those which carry it from the heart being named **arteries**, and those which return it to the heart being named **veins**; while between the arteries and the veins the blood flows through the system of **capillary vessels**, a close network of hair-like tubes, which distribute it among the elements of the tissues. The circulatory system, then, consists of a central propelling organ, the heart, and a series of vessels leading to and from the peripheral parts. It requires to be emphasised, however, even in an anatomical description, that though the heart is the motive power it is not the whole mechanism of the circulatory system and the vessels merely inert tubes; the vessels have mechanisms of their own, and these may be active in extremely localised areas of the body and with such effect as not only to influence the normal functions of the part but even to determine pathological changes in its structure.

The general plan of the vascular system is shown in fig. 1. In it two great arteries are seen to leave the heart, the one, the **pulmonary aorta** (P.A), usually named the **pulmonary artery**, and the other, the **systemic aorta** (A), usually named simply the **aorta**. The pulmonary artery divides into the right and left pulmonary arteries which distribute the blood to the capillary systems of the lungs (L, L); from these systems the blood is returned to the heart by the **pulmonary veins** (V, V). There is thus formed, by these vessels and the chambers of the heart from which the pulmonary artery arises and into which the pulmonary veins return, a **pulmonary circulation** which is complete in itself. The systemic aorta gives off a large number of branches which distribute the blood to the capillary systems of all the other parts of the body.[1] The first branches (B.C) are distributed to the head and neck and the upper limbs, and the blood they carry, after passing through the capillary systems of these parts, is returned to the heart by the **superior vena cava** (S.C). The aorta then passes downwards through the thorax into the abdomen and supplies branches to the walls of this cavity and to the viscera

[1] There also arise from the aorta or its branches small arteries which are distributed to the lungs; but for the present discussion these are omitted.

contained in it, and ends in vessels which proceed to the pelvis (I) and to the lower limbs (F); and the blood which is carried in these branches is returned to the heart by the **inferior vena cava** (I.C.). The systemic aorta and the two venæ cavæ and the chambers of the heart with which they are connected thus form a

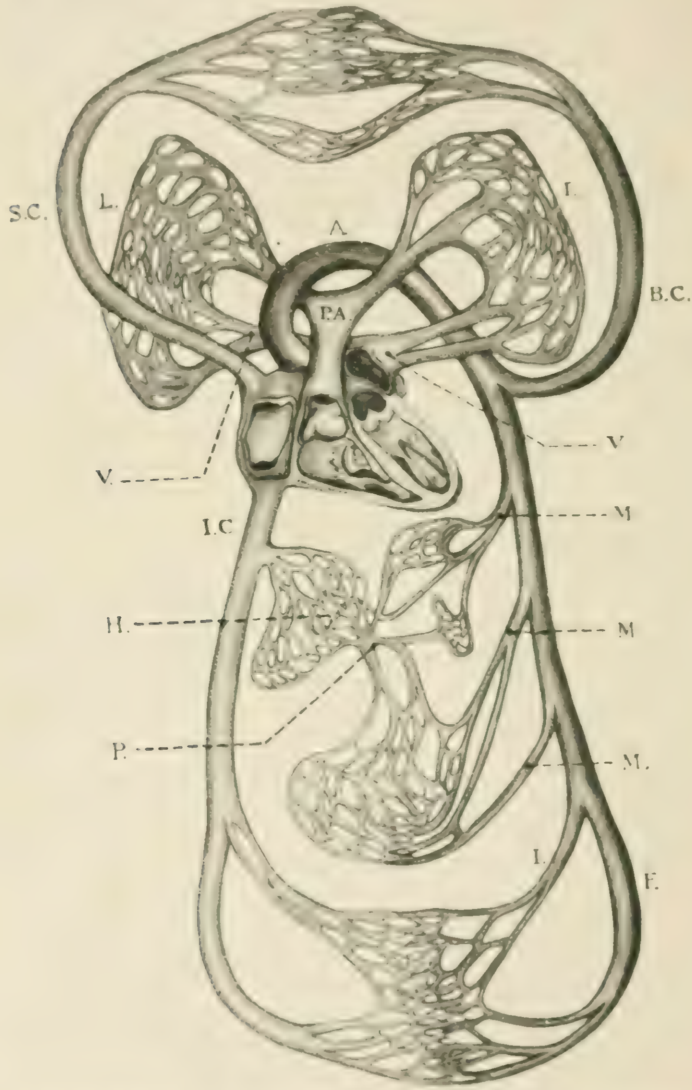


FIG. 1.—A SCHEME OF THE VASCULAR SYSTEM. (After BENNINGHOVEN.)
The explanation is in the text.

systemic circulation which is distinct and separate from the pulmonary circulation.

The superior and inferior venæ cavæ enter the same chamber of the heart which has, therefore, four chambers, namely, the right ventricle from which arises the pulmonary artery, the left atrium which receives the pulmonary veins, the left ventricle from which arises the aorta, and the right atrium which receives the two venæ cavæ (fig. 1).

One part of the systemic circulation, that of the abdominal alimentary viscera, requires to be specially mentioned. It will be noted (fig. 1) that the arteries distributed to these viscera (M, M, M) terminate in capillary systems in the usual manner, but the veins which arise from these systems (P) do not directly join the inferior vena cava but end in a common trunk, the **portal vein,** which passes to a further capillary system in the liver (H); and from this system veins pass to the inferior vena cava. This part of the systemic circulation, which begins and ends in capillary systems, is known as the **entero-hepatic** or **portal circulation**.

A **portal system** is said to be formed when a vein arising from the capillaries of a part instead of uniting with other veins and proceeding towards the heart breaks up into a second set of capillaries in another organ. The particular example described above is therefore the **hepatic** portal system, but other portal systems may exist, for example, the renal portal system in the majority of fishes.

There remains to be mentioned as part of the circulatory system another system of vessels, the **lymph vessels**, which contain the lymph, a fluid which permeates all the tissues and is present in various spaces in the body. The lymph vessels begin, like the veins, in networks of capillaries, and in their course towards the heart unite with one another to form larger trunks. The further course of these trunks is interrupted by one or more series of **lymph glands**, through which the lymph is filtered; but having emerged from these glands, the lymph vessels ultimately join with one another to form three or four large trunks which open into the systemic veins, chiefly the branches of the superior cava, not far from the heart.

There will be considered in this volume the descriptive anatomy of the heart and of the principal blood vessels and lymph vessels which are distributed to it. The account of the minute structure of the heart is given in Vol. II., Part I., which treats of "General Anatomy," while its development is considered in Vol. I. Much work has been done in recent years on the structural details of the heart, and to appreciate its bearing some knowledge of the comparative anatomy and development of the organ is necessary. A summary account of the relevant data yielded by comparative anatomy and by embryology will therefore be given by way of introduction to the description of the human heart.

COMPARATIVE ANATOMY OF THE HEART

The heart is a rhythmically contractile muscular organ which, during the intervals between its contractions, receives in its **atrial** chambers blood from the veins; and these chambers, having been filled, contract and the blood passes into the **ventricles**, which contracting in their turn project the blood into and along the arteries.

The most primitive heart is tubular in shape and contracts in peristaltic waves from behind forwards. The heart in many of the Annelida, for example, is of this form, and is indeed but a short expanded part at the anterior end of the dorsal blood vessel. In its wall there are smooth muscle fibres in the form of arched rings; these fibres contract successively, fibre after fibre, in such a way that the movement of the tube resembles the peristaltic movement of the gut. The hearts of adult Arthropoda, which are well-defined structures of specialised form, contain striped muscle; in some species (in many Insecta) the contraction consists of a slow peristaltic wave, while in others (in most Crustacea) the whole heart contracts

simultaneously. The embryonic heart of the Arthropoda, however, resembles the heart of worms. (Much attention is now being given to the heart of invertebrates; a review of the recent literature is given by CLARK.[1])

In *Amphioxus* there is no definitive heart. The larger blood vessels, however, have peristaltic contractile movements, and the sub-pharyngeal vessel corresponds to the heart and ventral aorta of the Craniata; it receives behind the hepatic vein from the hepatic cæcum and gives off along its course branches to the primary pharyngeal bars.

The heart of the Craniata is thus the hinder part of the sub-pharyngeal vessel, the wall of which has become highly muscular to propel the blood through the respiratory apparatus. In all the Craniata, however, the simple tubular heart is divided transversely to its long axis into four successive chambers, which from behind forwards are named **sinus venosus**, **atrium**, **ventricle**, and **bulbus cordis**. In *Ammocœtes*, the larval form of the lamprey (*Petromyzon*), the heart is so formed (fig. 2); the sinus venosus receives the portal blood from the liver, and from the bulbus cordis the ventral aorta passes forwards to distribute the blood to the branchial chambers. There is sometimes mentioned as a fifth segment of the heart the **atrial canal**, a short narrow cylindrical passage between the atrium and the ventricle, which though not distinguishable in the adult can be seen in the embryonic heart; as the heart develops the atrial canal becomes surrounded by the backward growth of the ventricle towards the atrium, so that it is, as it were, invaginated into the ventricle and lies on its inner surface outside the atrio-ventricular valves. (See further, "The Development of the Atrio-ventricular Valves.")

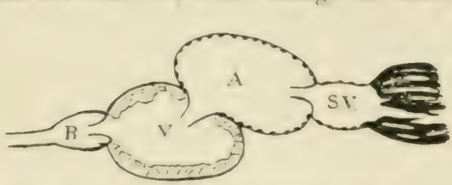


FIG. 2. THE HEART OF *Ammocœtes* IN LONGITUDINAL SECTION. (After KEITH.)

The constricted parts between the successive chambers, however, are to be looked on as sphincteric in function, closing the openings between the chambers; and the atrial canal is the best-developed sphincter. The distal part of the bulbus cordis is of the same nature. (See further, "The Morphology of the Connecting Musculature.")

In its further evolution, and associated with changes in the respiratory apparatus, the heart undergoes a division parallel to its long axis into bilateral halves, so that within it the pulmonary and general body (systemic) circulations are separated from one another. This division affects the second, third, and fourth parts of the tubular heart, but not the sinus venosus (see p. 37), and can be followed gradually in its successive stages through the vertebrate series until it reaches its completion in the birds and the mammals; and in the development of the human heart these phylogenetic processes of division can be followed with considerable fulness.

Fishes.—The heart in fishes is a simple tubular structure divided into the four primary parts, sinus venosus, atrium, ventricle, and bulbus cordis (fig. 3). The sinus is the most posterior part. It collects the blood from the veins of the whole body and to the continuous flow of this stream it acts as a block; for the forward movement of the blood from it into the atrium is discontinuous and is the result of its contractions. The contraction of the heart in fishes begins, therefore, in the sinus; and this is of great significance, for the sinus remains the initiatory area of cardiac contraction in all the higher vertebrates even when it has lost its independence as a separate chamber. The wall of the sinus in fishes, it should

[1] The works of the authorities cited are given in the list at the end of the volume.

be mentioned, is composed for the most part of fibrous and elastic tissues, only a few muscle fibres being interspersed. (See further, "The Morphology of the Connecting Musculature.") Chromaffin cells have been described in the dorsal part of the sinus in Cyclostomata between the myocardium and endocardium (Giacomini, *Monit. Zool. Ital.*, ann. 13, 1902). The opening of the sinus into the atrium is generally transverse to the long axis of the heart; it is guarded by a valve of two cusps, the **sinus** or **venous valve**. The atrium is a comparatively thin-walled chamber, expanded laterally in the form of appendices. The opening from it into the ventricle, the **atrio-ventricular opening**, is guarded by an **atrio-ventricular valve** which, primarily, consists of two cusps; these are of the semilunar type and without chordæ tendineæ or papillary muscles. The ventricle is characterised by its thick muscular wall, for it is the essential propulsatory chamber of the heart; the muscle fibres, as in all vertebrates, have cross striations and anastomose with one another. In fishes generally, the ventricular muscle is in the form of a fine trabecular network, on the superficial surface of which there is a thin layer of compact cortical muscle (fig. 4). This condition of the musculature of the ventricular wall is of interest, for it appears to be the primitive one; in Amphibia the condition is somewhat similar, but in reptiles the cortical musculature is relatively increased and the trabecular formation diminished; and in mammals the amount of the cortical muscle is very much greater and the trabecular network is reduced to a comparatively narrow strip of the whole thickness of the wall. By the contraction of the ventricle the blood in it is thrown into the bulbus cordis. This part of the heart varies very much in its size and form in the different classes of fishes, and as there is still a rather imperfect knowledge of its developmental history some confusion prevails in its nomenclature (Langer, Gegenbauer, Greil, Graham Kerr). The names which have been used for it are conus arteriosus, bulbus arteriosus, truncus arteriosus, and bulbus cordis. **Conus arteriosus**, however, is now used in human anatomy for a definite part of the right ventricle (p. 50). **Truncus arteriosus** is the name now usually applied in human embryology to that part of the common ventral vessel from which the pulmonary aorta and the proximal part of the systemic aorta are derived and the structure of whose wall, from the beginning, is that of a vessel. In the Teleostei this section of the ventral vessel is enlarged and its wall is thickened by a great development of smooth muscle and elastic tissue fibres, but it is entirely free of cardiac muscle; the name **bulbus arteriosus** is then used for it (fig. 3). The name **bulbus cordis** is thus the most suitable to be applied to that region which is the most distal part of the heart and which yet forms the most proximal part of the exit tube from the heart; and it is to be considered a cardiac chamber, for in its interior it carries the bulbar

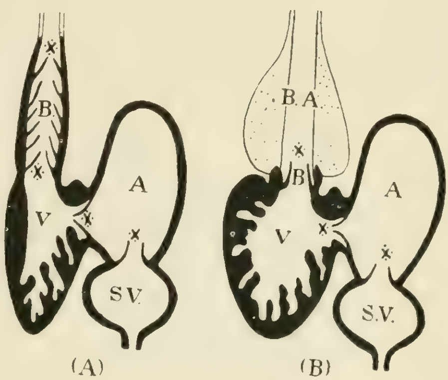


Fig. 3.—Longitudinal sections, diagrammatic, of the heart of (A) an elasmobranch fish, with well-developed bulbus cordis, and (B) a teleostean fish, with reduced bulbus cordis and well developed bulbus arteriosus. Cardiac muscle is present in the parts in solid black. (After Boas.)

A., atrium; B., bulbus cordis; B.A., bulbus arteriosus; S.V., sinus venosus; V., ventricle; X., valves.

valves and in its wall there is cardiac muscle. It is present in all vertebrate embryos, but in most forms it undergoes an ontological retrogression through the absorption of its proximal part into the ventricle and of its distal part into the truncus arteriosus; it remains persistent as a clearly separable chamber of the heart only in Elasmobranchii, Ganoids, Dipnoi, and Amphibia. The **bulbar valves** are arranged in horizontal rows and are most numerous in Elasmobranchii and Ganoids; there is a tendency, however, for the more posterior valves to disappear and in the vast majority of Teleostei only those of the most anterior row remain, for in the Teleostei the bulbus cordis has undergone reduction (fig. 3).[1]

The future division into pulmonary and systemic hearts is foreshadowed in the fish heart, for frequently the vein of the swim bladder opens separately into the sinus venosus; and in the Dipnoan heart the opening of the vein from the lung is found in the roof of the atrium entirely separated from that of the sinus. Here also the atrium is partially divided into right and left chambers by an incomplete septum which is formed in part by the cusps of the sinus valve. In *Lepidosiren* there is also an incomplete ventricular septum. The bulbus cordis is spirally twisted and is subdivided into two tubes by an incomplete septum, formed by a fusion of the bulbar valves (RÖSE). There are thus formed in the Dipnoi two parallel series of cardiac chambers, of which one has its origin behind in the sinus venosus and transmits venous blood to the posterior branchial vessels, while the other commencing with the left atrium conveys arterial pulmonary blood to the two anterior pairs of branchial vessels.

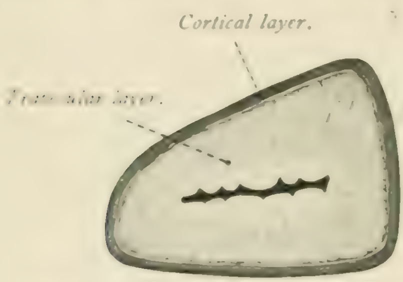


FIG. 4.—TRANSVERSE SECTION OF THE VENTRICLE OF THE COD, AFTER PROLONGED FIXATION.

Amphibia. The cavity of the atrium of the amphibian heart is divided into right and left parts by a thin septum. This is attached to the roof and posterior wall of the atrium, but it ends below over the common atrio-ventricular opening in a free arched border. The septum is thus incomplete, but it seems to vary considerably in size even in the same species (at least in *Rana esculenta* and *R. temporaria*); in some forms and especially when it is most complete (Salamander) the upper part of it is perforated. The sinus venosus, collecting the veins of the systemic circulation, opens into the right atrium, the opening being guarded by the sinus valve of two cusps, while in the left atrium there is the unguarded opening of the **pulmonary vein**; this vein runs over the middle of the sinus and enters the atrium close to the left side of the septum. The blood from both atria passes through the common atrio-ventricular opening into the left side of the common ventricle, the opening being guarded by a valve of two considerable cusps which are less membranous than in fishes and are attached to the ventricular wall by cords. The mixing of the two streams in the ventricle is greatly hindered by the trabecular formation of its musculature and the almost cavernous-like condition of its cavity. The trabeculation is evenly arranged in the lower Amphibia, but in some of the higher forms, for example, in the frog, owing to differences in the density of the trabeculation the right side of the ventricle appears darker than the

[1] In certain of the Teleostei (Albulidæ) the bulbus is visible from the exterior of the heart and there are two rows of valves in it. (BOAS; SMITH, *Anat. Record*, vol. xv., 1919.) PARSONS (*Brit. Assoc.*, 1928) has shown that the bulbus arteriosus is intra-pericardial in position.

left when the heart is full of blood. The bulbus cordis arises from the right side of the ventricular cavity. There are proximal and distal rows of valves in it in some forms (*Menobranchus*) and a single row in others (*Rana*). The two streams of blood are still kept considerably separated in the bulbus by an incomplete spiral septum, formed by the valves, in its interior, and they are thus distributed almost in their entirety to the systemic and respiratory circulations respectively. (For the mechanism of the heart of the frog, see GAUPP; and for a detailed description of the heart and valvular mechanism of *Ceratophrys*, see RAU, *Jour. Anat.*, vol. lviii.) As in fishes there are no true blood vessels of the heart wall, though small coronary arteries, arising from the first aortic arch, are distributed to the bulbus in most Amphibia; a coronary vein, however, has been described in *Cryptobranchus*. (The comparative anatomy and development of the amphibian heart are described by BENNINGHOFF, *Morph. Jahrb.*, Bd. li.)

Reptiles.—In reptiles, as in fishes and amphibians, the heart lies straight in the thorax, parallel to the long axis of the body, and not obliquely as in mammals. The apex of the ventricle in many reptiles (except snakes), and also in several amphibians and some fishes, is connected to the parietal pericardium by a ligament

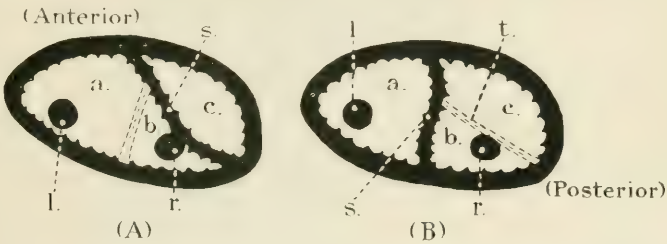


FIG. 5.—DIAGRAMMATIC TRANSVERSE SECTIONS OF THE VENTRICLE IN (A) THE REPTILIA GENERALLY, AND (B) IN THE CROCODILIA.

l.l. and r.r., left and right atrio-ventricular openings; s., ventricular septum; t., trabecula septo-marginalis; the apical septum lies between a and b, fig. A.

of definite structure which occasionally transmits blood vessels (**gubernaculum cordis**, FRITSCH). This ligament is remarkably constant in the species in which it occurs, though it may be quite absent in nearly related forms. It has been described as a pathological condition, like the lateral folds sometimes found in frogs, but this is incorrect and it should be considered a definite functional structure. It receives the superficial muscle layer of the ventricle (SHANER, *Anat. Record*, vol. xxix., 1925).

There is no separate bulbus cordis in reptiles. Three vessels, each having a definite wall, spring from the ventricle. They are the pulmonary artery, which arises from the right side, and the right and left systemic aortæ, the left aorta arising on the right near the pulmonary artery and the right aorta arising on the left; the presence of two separate aortæ is a reptilian character.

The division of the heart is further advanced in the reptiles than in the amphibians. The atrium is divided by a complete septum into right and left chambers which are entirely separated from one another; and each has its own opening into the ventricle which is guarded by a valve of a single cusp attached to the septal wall of the orifice (fig. 7). The sinus venosus lies on the dorsal wall of the atrium. It varies very much in its size in different species, in some (*Emys*) being a large and distinct chamber, and in others (*Chelonia canana*) small and scarcely more than the junction of the veins. The orifice is on the dorsal wall of the right atrium; in

fishes and amphibians it is generally transverse, but in reptiles it is usually oblique, the right end being higher than the left (figs. 6 and 7). The sinus valve consists of two membranous cusps, usually of equal size, which are fused below and on the left with the atrial septum and above and on the right fuse with one another and are continued into one or two strong musculi pectinati, through the contraction of which the cusps are probably fixed while they are approximated. The pulmonary vein is a single stem, short in most forms, but of considerable length in snakes, and opens into the left atrium close to the septum; the orifice is unguarded, though a valve of a single cusp was described by SABATIER in *Python* (*Études sur le cœur* ... *Annal. d. Sc. nat.*, 5me sér., T. xviii., 1873).

The ventricle, in whose wall there is still a considerable trabecular formation,

FIG. 8. INNER VIEW OF THE HEART OF A LIZARD. (From a preparation by Dr. Mackenzie.)

possesses a septum, formed apparently from fused trabeculae, which varies very greatly in its size in different species; it is smallest in the tortoise, where the ventricle is only very partially divided, and largest in the crocodile where it is complete, and the two ventricles are, therefore, quite separated from one another. In the Reptilia generally, then, the Crocodilia alone being excepted, the septum is incomplete. It runs obliquely from in front backwards and to the right (fig. 6, A). The ventricular cavity is thus more or less divided into two parts, the smaller of which lies in front and to the right and the larger behind and to the left; but in the lacertilian heart the two parts are in free communication over the upper concave edge of the septum (fig. 8). Both atria open into the left or posterior ventricle, the right auriculoventricular opening being close to the left or posterior surface of the septum. The two systemic aortae arise from the posterior chamber, while the pulmonary artery arises from the right or anterior ventricle. The apical region of the posterior chamber is traversed, in an almost sagittal direction, by a trabecular formation which runs from the back of the septum to the posterior wall of the ventricle and divides this region into a larger left and a smaller right portion

(fig. 5, A). In the Crocodilia this trabecular band is very greatly enlarged, and with the anterior part of the original septum and an incorporated endocardial cushion element from the region of the atrio-ventricular valves forms the new and complete **ventricular septum**, which is attached above between the atrial orifices (fig. 5, B). At the same time, the part of the original septum behind the attachment of the trabecular band undergoes a retrogression and as a rudimentary structure, the **trabecula septo-marginalis** (TANDLER), traverses the right ventricle. It will afterwards be described as the homologue of the **moderator band** of the mammalian heart, and in the crocodile it obviously intervenes between that part of the right ventricle into which the right atrium opens and that part from which the pulmonary artery arises (fig. 5, B, b and c). In the crocodile the left aorta also arises from the right ventricle, but there is an extra-cardiac communication between the two aortæ, the foramen of Panizza, so that the arterial and venous blood are not yet completely separated. Each of the three great arterial channels is guarded by a valve of two semilunar cusps at its origin.

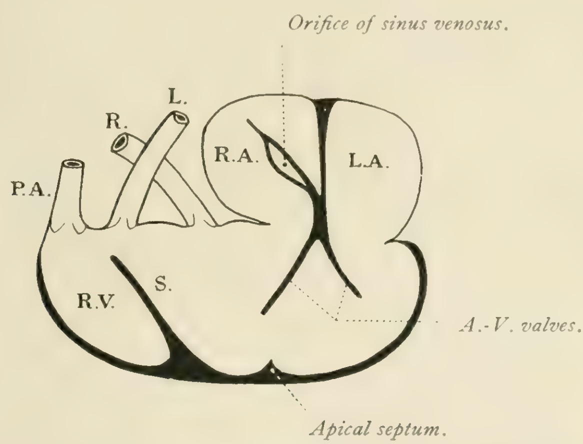


FIG. 7.—DIAGRAM OF THE HEART OF THE REPTILIA. (After SEDGWICK.)
R. and L., right and left aortæ; P.A., pulmonary artery; S., incomplete septum.

The phylogenetic origin of the left ventricle is by no means yet clear. It has been suggested, for example, that the right ventricular cavity of the higher Amniota represents the entire ventricular cavity of the Amphibia and that an extension of the right part of the cavity ultimately becomes the left ventricle. This extension is at first small and in *Monitor* is confined to the postero-dextral region of the ventricle; it occupies the entire posterior region in the snake, and in the *Chelonia* reaches the left side, the pulmonary artery and the right ventricle which originally occupied the ventro-sinistral region being pushed to the right in its advance. If this be so, the formation of the ventricular septum in the Reptilia, and its homologue the septum inferius (HIS) in man, would appear to be due to the extension of the ventricular cavity into the posterior cardiac wall rather than to its own ingrowth, as is described above and in the next section. The septum would be rotated forwards as the extension of the ventricular cavity increased, and in its right-hand surface we would be dealing with the postero-internal boundary of the Amphibian ventricle. It appears to the present writer, however, that the ventricular septum in the Crocodilia (and in the hearts of birds and mammals) consists of two parts, the one of which, the anterior part, represents the division of the ventricle to effect

a separation of the outgoing blood, and the other, the posterior part, the division to maintain the separation of the incoming atrial blood. The former of these parts appears first, and apparently is that found generally throughout the Reptilia, while the latter remains small and is largely replaced by the atrio-ventricular valves. Further work, however, is needed to maintain that in some forms the posterior part may not be present at the expense of the anterior part, and that the chambers which are named right and left ventricles are always really homologous cavities; but both parts it would seem are ingrowths into the common ventricle of the Amphibia.[1]

Birds.—In birds, as in mammals, the atrial and ventricular septa are complete and the right and left hearts are entirely separated from one another. The heart, conical in shape, lies in the long axis of the body behind the middle of the sternum; its base is directed cranially, while its apex lies between the lobes of the liver, the diaphragm, as a rule, not being so far developed as completely to separate the thorax from the abdomen. It weighs as much as $\frac{1}{50}$ to $\frac{1}{100}$ of the body weight, the proportion in reptiles being [illegible] to [illegible]; and on an average the heart in birds is nearly twice as heavy as in mammals of the same weight.

The right atrium receives the venous blood of the body. It is more capacious than the left atrium (in the proportion of 5 to 3), but its walls are distinctly thinner. It is divided internally, more distinctly than it is in mammals, into two parts, the sinus and the atrium proper; but, on the other hand, it is to be noted that the sinus is absorbed into, and forms part of, the chamber as does not occur in the Chelonia. Three veins open into the sinus, there being as in reptiles two anterior venæ cavæ, but the orifices of these veins vary in their relationships to one another in different species. The right superior cava opens into the upper right anterior part of the sinus, though it may open with the inferior cava (*Columba*), and the left superior cava, after winding round the posterior surface of the left atrium, opens into the lower back part of the sinus, though it may with the right cava open with the inferior cava (*Struthio*). In the vestibule of the left superior cava lies the orifice of the coronary vein, guarded by a small flap valve; but in a few forms this vein opens separately into the atrium. The right and left caval orifices are guarded by small flaps, membranous or muscular in their structure. The orifice of the inferior cava lies between the openings of the two superior cavæ, and is guarded on the left by a broad fold which projects into the atrium and intervenes between it and the left superior cava. The whole sinus area is limited in front by two strong muscular folds which surround its orifice; these folds are homologous with the sinus valves in reptiles. They commence on the roof of the atrial part of the chamber in a strong muscular fold, which stands out from among the musculi pectinati among which it lies; this fold expands into the two valvular folds, that on the left side of the sinus terminating at the lower part of the fossa ovalis and that on the right side terminating on the floor of the atrium after passing round the right side of the inferior cava. The base of the latter fold is highly muscular, and from it the majority of the musculi pectinati of the atrium arise. The left atrium consists of two parts: (1) a right posterior smooth part, which receives the right and left pulmonary veins, one on each side; and (2) a left anterior part, the walls of which are richly covered with musculi pectinati. The two parts are separated by a semilunar septum growing from the dorsal and upper wall of the atrium; it is absent, however, in the *Passeriformes* and varies in its height in other forms, and in none is it sufficiently large to act as a valve. The atrial septum

[1] [For further work on the Reptilian system, O'Donoghue, "The Heart of the Leathery Turtle," *Journ. Anat.*, vol. lii., 1918; Goodrich, "On the Classification of the Reptilia," *Proc. Roy. Soc.*, B, vol. lxxxix., 1916; "Note on Reptilian Heart," *Journ. Anat.*, vol. liii., 1919.]

is membranous and seldom contains muscle fibres. In the middle of it there is a thinner transparent region which is not depressed but which corresponds to the fossa ovalis in mammals. In the embryo this region is cribriform (see PATTEN, *Anat. Record*, vol. xxx., 1925), this condition replacing the single foramen ovale of the mammalian fœtus. ROKITANSKY, however, has described conditions of the mammalian septum which resemble that of birds, see p. 13.

The right ventricle does not reach to the apex of the heart. Its wall is one-third the thickness of that of the left ventricle. It is smooth in its interior except at its antero-inferior part, where there is a rich fine trabeculation passing from the septum to the anterior wall; the left ventricle, on the other hand, possesses numerous trabeculæ, except over the septum, and from some of these chordæ tendineæ arise and pass to the mitral valve. The mitral valve, of two or three cusps,[1] resembles that of mammals, but the right atrio-ventricular orifice is guarded by a muscular fold which is quite different from the tricuspid valve of mammals. This fold, as thick as the wall of the ventricle, passes from the right side of the orifice of the pulmonary artery downwards and backwards round the atrio-ventricular orifice to the junction of the septum and the posterior wall of the ventricle. The convex free edge of the fold, to which no chordæ tendineæ are attached, is turned towards the septum and is applied to it during ventricular systole. The pulmonary artery and the aorta are each provided with three semilunar cusps at their origin.

Mammals.—In Monotremes (*Ornithorhynchus*) and Marsupialia (*Dasyurus*) the heart lies in the long axis of the body and in the middle line. It also occupies this position in some pronograde placental mammals (cat), but in others (squirrel) it lies obliquely downwards, forwards, and to the left. The differences in position are said to be related to differences in the form of the thorax (TANJA). It is sometimes held that in all pronograde Placentalia the pericardium and the diaphragm are separated from one another by a larger or smaller interval, as in the horse and the sheep, and that only in anthropoids and man are these structures fused (p. 130); fusion, however, has been described in several other forms (*Lemur mongoz* and many Quadrumana, LECHE; pig, MÜLLER). The space between the pericardium and the diaphragm, when it is present, is occupied by the infra-cardiac lobe of the right lung.

Right Atrium.—The sinus venosus cannot be distinguished from the exterior as a separate chamber of the mammalian heart. In Monotremes the three cavæ, the right and left anterior and the posterior, open separately into the right atrium. The three orifices are surrounded, however, by the two cusps of a common **sinus valve**, so that in the interior of the atrium the sinus area can readily be defined. The cusps, which are somewhat rudimentary round the upper right cava, are closely approximated to one another between the orifices, but are not fused (fig. 8). The descriptions of these cusps given by RÖSE and by BORN differ in their details; the figure given here is from two specimens of *Ornithorhynchus* in the writer's possession. In the base of the upper part of the right cusp, in front of the right superior cava, there is a distinct muscle band; this represents the upper part of the **crista terminalis** of man and part of the sphincter muscle of the sinus valve of reptiles. The heart veins open directly into the heart in the **spatium inter-septo-valvulare**, a considerable space and diverticulum which lies between the left sinus valve and the septum, and the mouth of which is bounded on its valvular side by a distinct muscle ring, the isthmus Vieussenii (fig. 8). The atrial septum opposite this ring has a network appearance (fig. 8) and, as was shown by

[1] This is the description of OWEN and CUVIER, but that three cusps are almost invariably present was shown by HODGKINSON (*Jour. Anat.*, vol. xxxv., 1900).

Hochstetter, in *Echidna* it is a perforated sieve-like membrane in the embryo, there being no foramen ovale. In *Echidna* the ventricular veins open into the posterior cava. In Marsupialia the sinus valve formations are absent, apart from one or two trabeculæ in front of the right superior cava, and the sinus region can be distinguished from the rest of the atrium only by its smoothness; in the embryo, however, there is a distinct sinus with two large valve cusps. The spatium intersepto-valvulare is also absent and there is no distinct annulus ovalis. As in Monotremes there is no foramen ovale, but there are several perforations in the atrial septum. In Monotremes and Marsupialia there is a cross anastomosis in the upper part of the thorax between the two anterior cavæ, but the left cava still conducts the blood of the left side to the heart: in the Placentalia, however, this

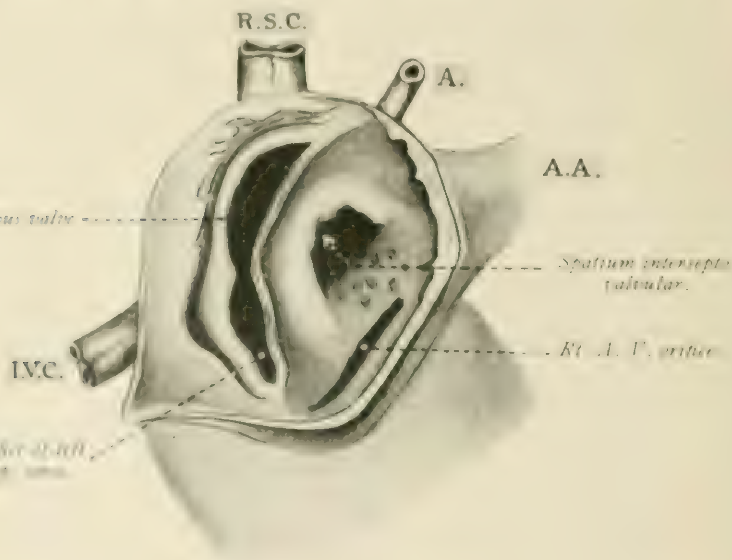


Fig. 8.—The right atrium of *Ornithorhynchus*.
A., aorta; A.A., right atrial appendix; I.V.C., inferior vena cava; R.S.C., right superior cava.

anastomosis carries the blood of the left side to the right cava, and below it the left cava undergoes an atrophy [1] and persists only at its lower part as the **vein of Marshall** (see p. 107). This opens into the **coronary sinus**, which represents the left horn of the sinus venosus, and in Placentalia always receives the cardiac veins (p. 105). The venous openings in the right atrium in Placentalia are, therefore, the (right) superior cava, the inferior cava, and the coronary sinus. In Edentata the three openings are surrounded by membranous sinus valve cusps almost exactly as in Monotremes, but the lower part of the right cusp is best developed and forms a large fold in front of the orifices of the inferior cava and coronary sinus; there is also a small intersepto-valvular space between the left cusp and the septum. In all other Placentalia, with the exception of some Rodentia (*Mus*, sometimes *Cavia*), in which it remains distinct, and in the hedgehog (*E. europæus*, Leche) where the conditions

[1] A left cava is found in several groups, for example in Insectivora, Chiroptera, and Proboscidea.

are peculiar, the left valve is fused with the septum so that there is no intersepto-valvular space; but the musculature of its attached border assists in the formation of the **annulus ovalis**. The membranous part of the right valve persists only at its lower part and forms the **Eustachian** and **Thebesian valves** at the orifices of the inferior cava and coronary sinus; but these are absent in most Carnivora, Cetacea, and Chiroptera, and in some other forms, and in many species one or other may be wanting. The **foramen ovale** and its associated parts are formations typical of the embryo of placental mammals, that is, there is in them a single, definitely bounded opening in the atrial septum which is closed after birth by the apposition and fusion of its overlapping walls (see p. 39); Röse and Rokitansky, however, have described conditions of multiple perforations in the septum below the foramen ovale in the sheep and the horse which are closed by a proliferation of the endocardium. The right wall of the foramen ovale has a lower free margin, highly arched and concave downwards; with this wall the left sinus valve is completely fused (see exceptions above) so that the intersepto-valvular space is obliterated. The muscle ring of the isthmus Vieussenii becomes incorporated in the free edge of the septum and forms with it a distinct annular muscular formation, the **annulus ovalis**, which completely covers the foramen ovale; the annulus is best developed in the hearts of ruminants.

Left Atrium.—In Monotremes there is a single pulmonary venous stem formed by the right and left pulmonary veins, which, after a considerable interstitial course in the atrial wall, opens into a funnel-shaped part of the left atrium. In Marsupialia and Placentalia there are usually four pulmonary veins which may open separately, as in Primates, or after the two veins of one or both sides have fused; in *Halicore* alone, apparently, is there a single stem for the two sides. In the marsupials and in Edentates the pulmonary veins open into a funnel-shaped diverticulum, but in the higher placental mammals, with a few exceptions, as for example the rabbit, this diverticulum broadens more and more and forms the posterior wall of the atrium; and the orifices of the pulmonary veins of the two sides are, therefore, moved further and further apart.

Ventricles.—The ventricular septum is complete and, as a rule, of the same thickness as the wall of the left ventricle; this is generally considerably, even as much as four times, thicker than the wall of the right ventricle, but in Cetacea the right ventricle may be nearly as thick or thicker (*Hyperoodon*, Bouvier, *Ann. d. Sc. nat.*, Paris, 1892). The walls are usually set with muscular trabeculæ, but in some forms (the horse) they are smooth. The right atrio-ventricular orifice is guarded in *Ornithorhynchus* by a single lateral cusp, the septal cusp being absent (Röse) or very rudimentary (Lankester); in one of the writer's specimens, however, there is a distinct though small membranous septal cusp, and Beddard has described a complete cusp in two specimens. The lateral cusp is connected to the septum by three **papillary muscles** which are continued through the cusp to its attached margin. In *Echidna* the muscle fibres of the papillary muscles end at the margin of the cusp; and in this species there is a thin membranous septal cusp attached below to the ventricular septum. In Marsupialia and Placentalia the orifice is guarded by three cusps (two cusps in Chiroptera), a septal and two lateral, which are attached through chordæ tendineæ to papillary muscles or directly to the septum. The papillary muscles vary in their arrangement, but usually the largest muscle lies laterally, arising either from the septum or the lateral wall, a smaller one lies posteriorly, while the septal cusp is attached to the septum either directly by chordæ tendineæ or these may pass to small papillary muscles. The left atrio-ventricular orifice is guarded in Monotremes, as in birds, by three cusps, a medial and two lateral, which are invaded by the muscle tissue of the three

papillary muscles to which they are attached below; the medial cusp is the least muscular. In marsupials and placental mammals there is a **mitral valve** of two membranous cusps, the two lateral cusps being fused; and there are two papillary muscles, anterior and posterior, with chordæ tendineæ reaching to the cusps.

DEVELOPMENT OF THE HEART

The development of the *heart* has been fully described in Vol. I.,[1] but there will be included in this section a general statement of the process in order that certain parts of the descriptions which follow may be stated, as they can best be stated, in developmental terms.

It is not necessary, for the present purpose, to discuss the stages earlier than that in which, in a human embryo of five or six segments, the heart consists of a short endothelial tube, the **endocardial tube**, lying well within a mantle of splanchnic

FIG. 9.—THE HEART RUDIMENT IN A HUMAN EMBRYO OF 5-6 SEGMENTS. (Diagrammatic: after CORNING.)

N.P., neural plate; G, fore-gut; P P, pericardial cœlom.

mesoblast, the **myo-epicardial mantle**, and is placed in the forepart of the cervical region ventral to the fore-gut in a relatively large **pericardial cavity** (pleuro-pericardial cœlom) (fig. 9).[2] The myo-epicardial mantle develops into the muscle, **myocardium**, and the fibrous structures of the heart wall and its covering of visceral pericardium, the **epicardium**, while the endothelial tube becomes its endocardial lining.[3] The space between the endothelial tube and the myo-epicardial mantle is soon occupied by a delicate subendothelial reticulum, the exact source of which is not yet clear (see p. 28); and the spaces of the reticulum are filled with fluid. At a later period the myogenic cells proliferate and invade the subendocardial tissue, and form in it a muscular sponge-work to the inner surface of which the endocardium becomes applied. At its earliest appearance, in the higher mammals, the heart tube is slightly bent on its long

[1] See also the works cited there for His, Born, Mollier, Tandler, and Hochstetter, and among more recent works see Wilson, Waterston, Robinson, Mall, Frazer, Watt, Schaeffer. For an account of the development of the heart in lower vertebrates, see Graham Kerr.

[2] For a recent discussion of the early stages see Wilson, "Observations on Young Human Embryos," Jour. Anat., vol. xlvii., 1913.

[3] The endocardial tube shows contractile movements of its wall before these can be detected in the myo-epicardial mantle; for the physiology of the embryonic heart, see Born.

axis and has an S-shaped curvature (fig. 10); and it is already possible to distinguish its future subdivisions though these are more easily defined when the curvature of the tube is more strongly developed and when parts of it have increased in diameter. It is connected for a short time along its whole length to the ventral surface of the fore-gut by the **dorsal mesocardium** (fig. 9); but the greater part of the mesocardium is soon absorbed and the heart tube remains connected to the dorsal wall of the pericardium only at its posterior end, where it enters the pericardium (venous mesocardium), and at its anterior end, where it leaves the pericardium (arterial mesocardium), and between these two parts it forms a sling, or a loop, which is convex forwards and to the right and concave backwards and to the left (fig. 10). The dorsal mesocardium is complete in a 3 mm. embryo; the intermediate part is absorbed immediately after this (see WATERSON). The ventral wall of the pericardial cavity (**membrana reuniens** of RATHKE), which (in the mammals) is not connected to the heart tube at any

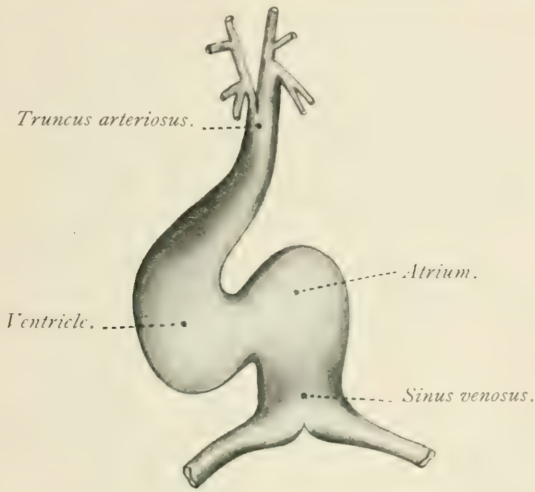


FIG. 10.—A DIAGRAM OF THE HEART TUBE IN AN EARLY HUMAN EMBRYO, SEEN FROM THE FRONT. (From the model by HIS.)

time,[1] is very thin, and for a considerable period contains neither skeletal nor muscular elements, but is formed by a layer of mesenchymatous tissue; and it will be readily understood that if it becomes broken the heart tube will be exposed on the anterior surface of the thorax.

In the next stages of its development the curvature of the heart tube becomes much more marked (fig. 11). This is due to (1) the growth of the free, sling-like part of the tube at a greater rate than its fixed ends separate from one another, and (2) to the unequal expansion of its lumen;[2] and, as results, the heart

---

[1] The pericardial cavity is at first, like the heart tubes, a double structure, and when they fuse a ventral interpericardial septum is formed; this is not, however, a true mesocardium. (See ROBINSON and WILSON.)

[2] It should be remembered, in all discussions of the significance of this curvature, that in lower vertebrates the heart tube at first is straight and then undergoes actual bending by a growth in length beyond the length of the rigid pericardium; and that this bending, of which the mammalian bending is a counterpart, is shown in the spiral formations of the bulbus cordis and truncus arteriosus (see further, GRAHAM KERR), and is reflected in the spiral arrangement of the ventricular musculature as opposed to the annular arrangement of the atrial fibres (WALMSLEY). BREMER, *Amer. Jour. Anat.*, xlii., 1928, has fully described the curvatures and has discussed their interpretation.

rudiment now fills a much greater part of the pericardial cavity, its several parts are defined, and its two ends are relatively approximated to one another. At its posterior end the heart tube is expanded transversely and receives in a common chamber the umbilical (allantoic) and omphalo-mesenteric (vitelline) veins and the ducts of Cuvier (which are formed, one on each side, from the anterior and posterior veins of the body wall); this chamber is the **sinus venosus** and it is, at this stage, embedded in the substance of the septum transversum. It is succeeded in the heart tube by the primitive **atrium** which lies in the back part of the pericardial cavity, close to its dorsal wall. At first there is no sharp boundary between the sinus and the atrium, and the opening between them is wide. Later, however, the opening is constricted from the left side; it becomes, therefore, relatively smaller and is shifted towards the right half of the atrium. It is then possible to distinguish in the sinus a centre transverse part and two (right and

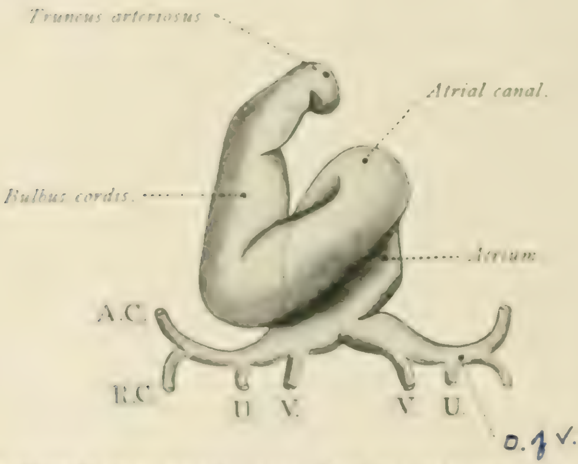


Fig. 11.—A diagram of the heart tube showing the increase in curvature and the early form and relations of the chambers.

A.C., anterior cardinal vein; R.C., posterior cardinal vein; U.U., umbilical veins; V.V., vitelline veins.

left) lateral horns which open into its extremities; these lateral horns receive the ducts of Cuvier (fig. 12). Beyond the atrium the heart tube is bent forwards towards the ventral wall of the pericardium (fig. 11); this bent part is known as the **atrial canal**, and in it the endothelial tube is constricted and the subendothelial tissue is increased in amount. The atrial canal is succeeded by the **ventricular loop**, the apex of which points forwards (ventrally), distally (caudally), and to the right. The proximal (downward) limb of the loop is the **ventricular** chamber of the heart, and the distal (upward) limb is the **bulbus cordis**, and the cleft between the limbs is the **bulbo-ventricular cleft**. The endothelial tube of the upper part of the bulbus is constricted and here, as in the atrial canal, there is an increase in the amount of the subendothelial reticulum. The bulbus cordis passes dorsally and, close to the ventral surface of the fore-gut, leads into the **truncus arteriosus**, which is the commencement of the arterial system. The **endothelial thickenings** which develop in the atrial canal and bulbus cordis are the primitive valvular arrangements of these parts; when the muscular walls contract they are pressed together and prevent the flow of blood through them. It is to be noted that in reference to the ventricle, of

which they are the guards, the former region will be contracted in ventricular systole and the latter in ventricular diastole.

In the next stages of the development of the heart the several chambers are further defined by growth changes in each of them and by alterations in position relative to one another. The sinus venosus rises out of the septum transversum and comes to lie on the dorsal surface of the atrium; and, associated with the caudal displacement of the whole heart, from the original position it occupied opposite the third and fourth segments to its ultimate position opposite the fourteenth to nineteenth segments, there is a change in the direction of the sinus horns and they now run downwards and medially towards the transverse centre part and form with it an arch convex caudally. The left horn lags behind the right horn in its growth and now is distinctly smaller (fig. 12). The communication

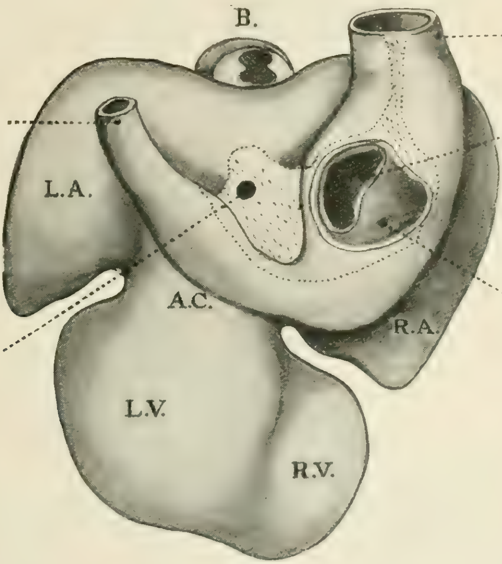


FIG. 12.—THE HEART OF A HUMAN EMBRYO, FROM BEHIND. (After the model by HIS.) B., bulbus cordis; A.C., atrial canal; L.A., R.A., left and right atria; L.V., R.V., left and right ventricles.

between the sinus and the atrium, now very much reduced in size, is a vertical (sagittal) slit in the dorsal wall of the right part of the atrium. Along the right side of the opening a fold is formed, growing from above downwards; this is the rudiment of the **right venous valve**. The **left venous valve**, along the left side of the opening, develops at a later period and, having formed, the two valves fuse with one another at the upper and lower ends of the opening; the upper fused ends are continued on to the roof of the atrium as the **septum spurium**, while the lower ends are continued to the atrial canal (fig. 13). The lateral parts of the atrium become very much expanded and form diverticula which pass from behind forwards (dorso-ventrally) round the distal part of the bulbus cordis (fig. 14). Opposite where the bulbus is in contact with it, the wall of the atrium is folded inwards towards the cavity in the form of a flat prominence which extends over the roof and loses itself on the posterior wall; this is the rudiment of the **septum primum** and is the first indication of the division of the atrium into right and left chambers. The sinus venosus opening is on the right side of the septum and the small opening of the single pulmonary vein

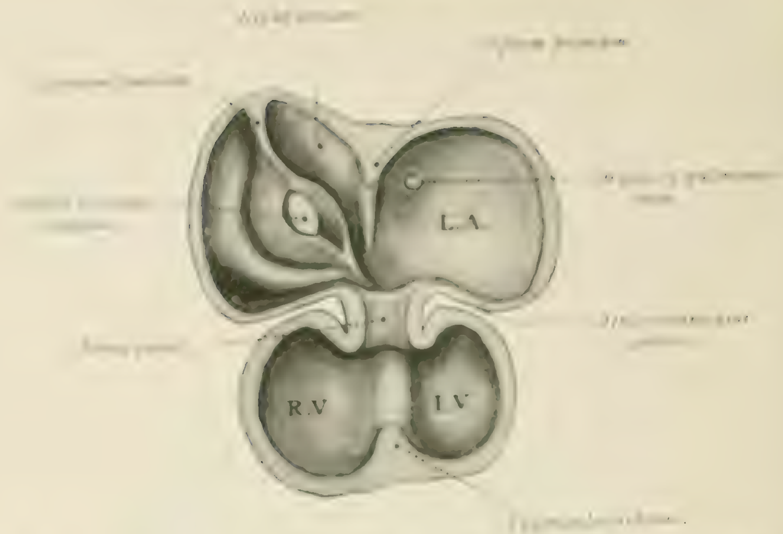


FIG. [illegible]—THE [illegible] HALF OF THE HEART OF A HUMAN EMBRYO, VIEWED FROM THE FRONT. (After [illegible] model by His.)

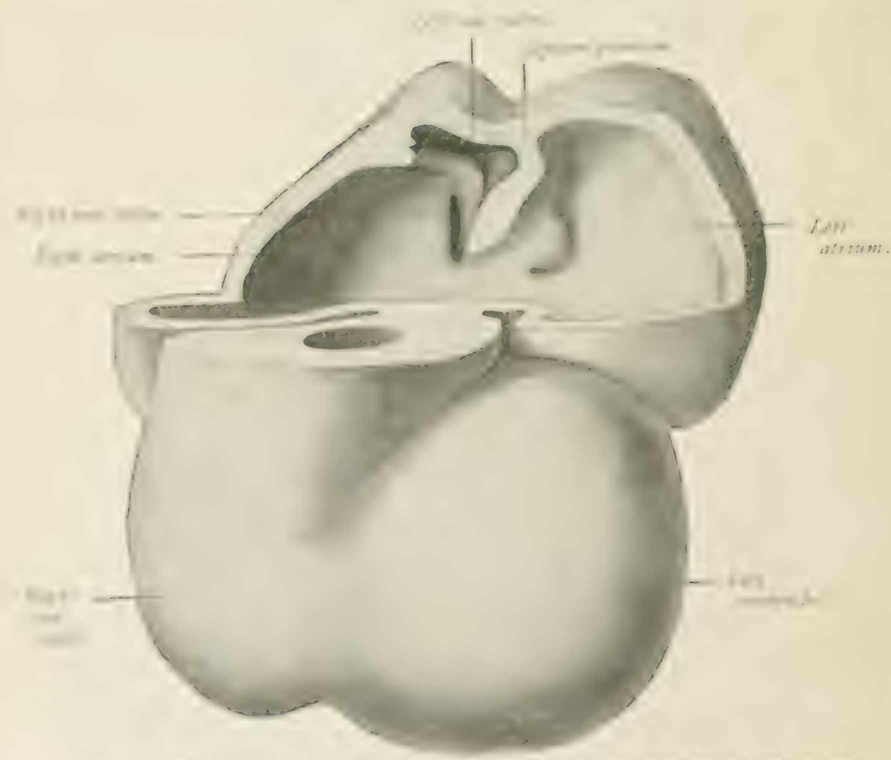


FIG. [illegible]—THE HEART OF A HUMAN EMBRYO OF [illegible] MM., VIEWED FROM THE FRONT. (After [illegible].)

[illegible] to show the septum primum and the valves guarding the orifice of the [illegible]. [illegible]

lies on its left side (fig. 13). The opening from the atrium into the atrial canal, which at first is circular and on the left side of the atrium, now becomes oval in shape, elongated transversely, and is placed in the middle of the floor of the atrium. The atrial canal is no longer visible on the surface of the heart; it is covered by the growth over it of the atrium from above and the ventricle from below, and these chambers come into contact with each other along the deep atrio-ventricular groove (fig. 13). The subendothelial reticulum of the atrial canal is greatly developed on its anterior and posterior walls and forms projections into its cavity which are named the **anterior** and **posterior endocardial cushions**. The apex of the ventricular loop by this time has passed down ventral to the atrium and is carried towards the middle line; the bulbo-ventricular groove thus becomes vertical and the ventricular chamber becomes the left limb and the bulbus cordis the right limb of the loop. At the same time, the whole loop is displaced to a position caudal to the atrium so that the atrium now lies on the dorso-cranial side of the ventricle and is crossed anteriorly by the bulbus cordis (fig. 14). The ventricular loop expands on both sides, and the originally

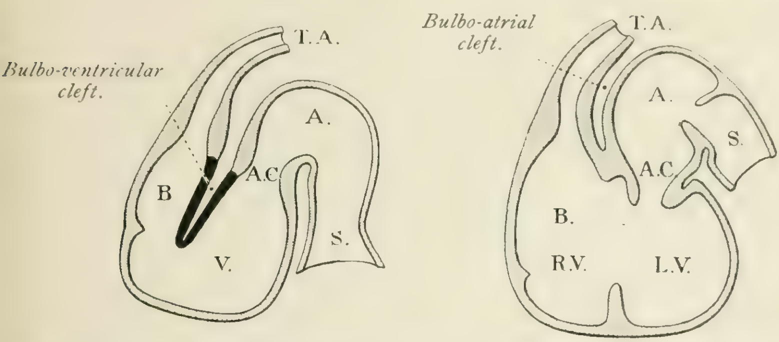


FIG. 15.—DIAGRAMS TO ILLUSTRATE THE REDUCTION OF THE BULBO-VENTRICULAR CLEFT AND THE FORMATION OF THE RIGHT VENTRICLE. (After KEITH.)

A., atrium; A.C., atrial canal; B., bulbus cordis; S., sinus venosus; T.A., truncus arteriosus.

small opening between its two limbs (ventriculo-bulbar opening) becomes very much larger; that is, the bulbo-ventricular cleft is absorbed and the dorsal wall of the bulbus passes into the ventral wall of the atrial canal at the bottom of a short **bulbo-atrial cleft** (fig. 15). There is now a common ventriculo-bulbar cavity into the left posterior part of which the atrial canal opens and from the right anterior part of which the distal part of the bulbus leads. In the floor of the common chamber a sagittally placed ridge appears. This is the commencement of the **ventricular septum** and is the first indication of the division of the ventricular cavity; its position is marked on the surface of the ventricle by a shallow sulcus, the anterior interventricular groove (fig. 14). It will be noted that the right ventricle is formed from the right portion of the transverse part of the primitive loop and its ascending (bulbar) limb, and is, therefore, a composite chamber; but there is no demarcation between its two parts in normally developed hearts. (See further, "Development of the Ventricles" and "Anomalies of the Heart.")

The relative position of the several parts now achieved is maintained through all the subsequent phases of the development of the heart. The further changes in the chambers will best be described after an account has been given of their adult form, and they are, therefore, included in the descriptions of them.

THE EXTERNAL FORM OF THE HEART

The heart is a hollow organ. Its walls are formed chiefly of muscle, the cardiac muscle or **myocardium**. Its cavity, however, is divided by a longitudinal muscular septum into right and left halves, and each of these halves is subdivided by a transverse constriction into two compartments, named, respectively, the **atrium** and the **ventricle**; and the wide opening through which these chambers

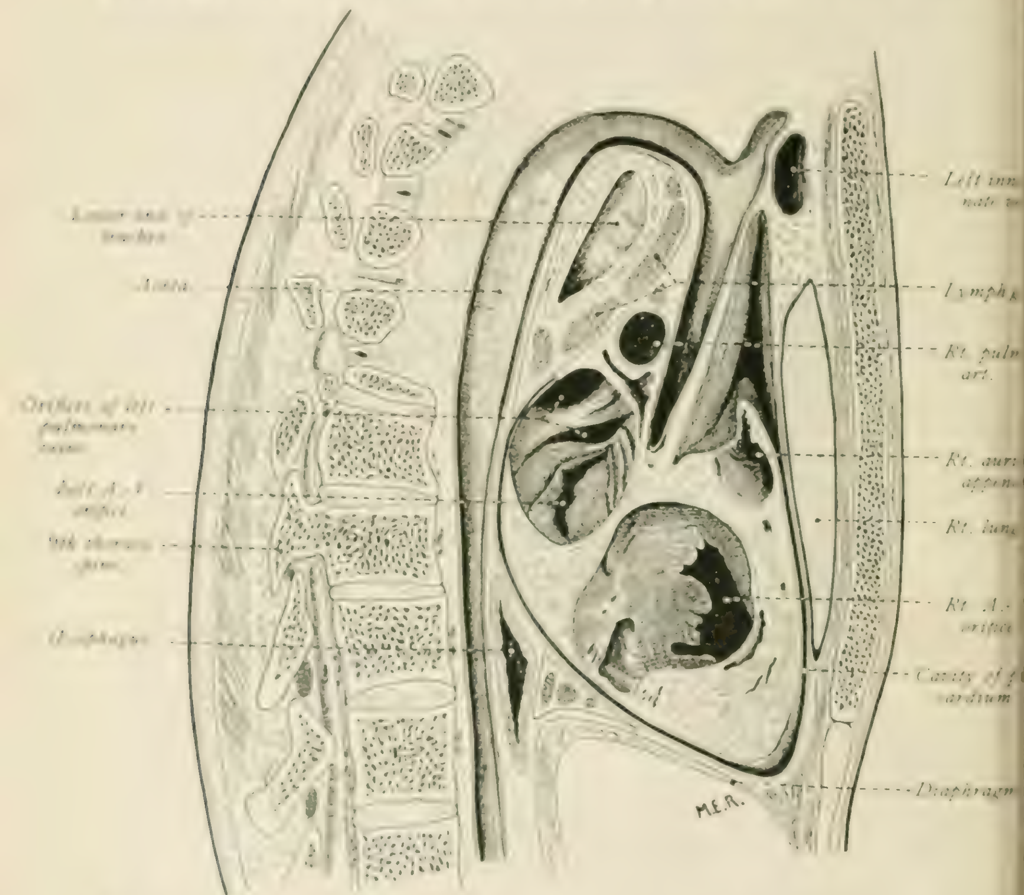


Fig. 16.—The left half of a sagittal section nearly in the median plane of the thorax of a man aet. 40 years. (The viscera are displaced downwards for a distance of about one vertebra.)

communicate with each other is named the **atrio-ventricular orifice** (ostium venosum, B.N.A.).

The general form of the heart[1] is that of a blunt cone, a little flattened from front to back and somewhat uneven on its surface. The broader end or **base** of the heart (basis cordis),[2] formed by the posterior surface

[1] The exact form of the heart depends, of course, on its functional state, that is, whether it is contracted or relaxed; the description given here refers to the distended or diastolic heart, examined in the thoracic cavity and without portion of the great vessels attached to it.

[2] This is not the "base of the heart" as defined in clinical medicine: the term, as used there, is applied to that part of the anterior surface from which the aorta and pulmonary artery arise.

of the atrial chambers, is directed backwards, upwards, and to the right, and is placed opposite the fifth, sixth, seventh, and eighth thoracic vertebræ; while the **apex** (apex cordis), bluntly rounded, points forwards, downwards, and to the left, and, under cover of the anterior border of the left lung and the pleura, lies deep to the fifth left intercostal space about $3\frac{1}{2}$ in. from the middle line. The heart, therefore, has a very oblique position in the chest; and indeed, as may be seen in fig. 16, the axis from the apex to the centre of the base lies more nearly in a horizontal than in a vertical plane;[1] it passes from behind forwards, downwards, and to the left. (On the external form of the heart in man and other mammals, see PATTEN.)

The heart is attached at its base to the great veins which enter its atria and to the pulmonary artery and systemic aorta which leave its ventricles, but otherwise it is entirely free and movable within the sac of the pericardium. It is customary to describe three surfaces on the heart, an anterior or **sterno-costal**

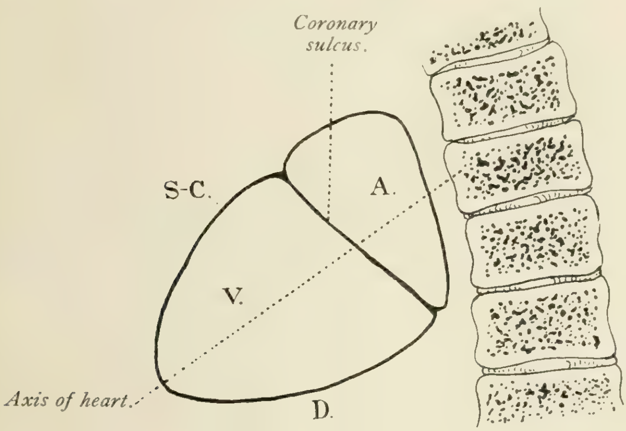


FIG. 17.—A DIAGRAM OF A LONGITUDINAL SECTION THROUGH THE HEART TO SHOW ITS SURFACES. The base is facing the vertebral column.

A., atria; V., ventricles; D., diaphragmatic surface; S.-C., sterno-costal surface.

surface, an inferior or **diaphragmatic surface**, and a posterior surface or **base**; the relative position of these surfaces is shown in fig. 17.

The anterior or **sterno-costal surface** (facies sternocostalis) of the heart (fig. 18), distinctly convex in its contour, looks forwards, upwards, and to the left. It lies behind the sternum and the third, fourth, fifth, and sixth costal cartilages, but for the most part it is separated from them by the pleuræ and the lungs and only a small part of it remains uncovered (fig. 73). This surface is divided into two parts by a deep groove which is placed much nearer the base than the apex of the heart, and which, while transverse to the long axis of the heart, is more nearly vertical in direction when the heart is in its normal position in the thorax; this is the anterior part of the **coronary** (atrio-ventricular) **sulcus** (sulcus coronarius) and, though obscured in part by the pulmonary artery and the aorta, clearly separates the atria above from the ventricles below. This sulcus is continued round the margins of the heart on to its posterior surface, where

[1] The usual descriptions of the heart, therefore, are conventional, for in them the heart is considered to be placed vertically with its apex downwards. In its normal position the long axis of the heart forms an angle of 55° with the vertical (HYRTL).

it intervenes between the base of the heart, formed by the atria, and the inferior or **diaphragmatic surface** (facies diaphragmatica), formed by the ventricles (fig. 17). The diaphragmatic surface is almost horizontal in position (PATTEN). It is much smaller than the sterno-costal surface. It is flattened, or at the most only slightly convex in the transverse direction, and it rests chiefly on the central tendon of the diaphragm, but towards the left to a small extent also on its muscle substance.

In the fetus and infant the atria extend on to and form part of the diaphragmatic surface of the heart. POIRIER describes the atria as forming part of the diaphragmatic surface in the adult, but the diagram to which he refers (from LUSCHKA) is a section of an infant of eighteen months. The lower end of the right atrium, into which the inferior vena cava opens, is the only part of the atrial portion of the heart which, in the adult, touches the diaphragm (fig. 19).

On the right and below, the sterno-costal and diaphragmatic surfaces are separated by a sharp and rather thin border, the **margo acutus**. This margin, usually a little concave in conformity with the curvature of the diaphragm, is almost horizontal in position and occupies the angle between the diaphragm and the anterior wall of the thorax. The coronary sulcus is deepened on it by the overhanging of the right atrium. The upper or left border of the heart, the **margo obtusus**, is shorter, thicker, and more rounded. In the diastolic heart it is so broad that it is better described as a surface than as a border; and since its relations are those of neither the sterno-costal surface nor the diaphragmatic surface, for it is directed to the left and related to the left lung and pleura, it is best named the "left surface of the heart" (POIRIER). It is more definitely separated from the diaphragmatic surface[1] than from the sterno-costal surface.

The coronary sulcus, it has been noted (fig. 17), separates the postero-superior **atrial portion** of the heart from the larger antero-inferior **ventricular portion**.

The **ventricular portion** of the heart is conical in shape, though somewhat flattened from front to back. Its base is directed upwards and backwards and is continuous with the atria behind, but in front it is free of them and is continued into the pulmonary artery and the systemic aorta (fig. 20). On the ventricular portion there are two longitudinal **interventricular grooves**, one on the sterno-costal and the other on the diaphragmatic surface, which extend from the coronary sulcus towards the apex and mark its division into right and left chambers. The anterior furrow (sulcus longitudinalis anterior), which appears from between the pulmonary artery and the left auricular appendix, but sometimes is scarcely to be defined, lies nearer to the left side of the heart, while the posterior furrow (sulcus longitudinalis posterior) lies nearer to the right side; and they are continuous with one another on the inferior border of the heart only a little to the right of the apex in a slight depression, the **incisura apicis cordis**. In the normal position of the heart, then, the **left ventricle** lies above and to the left and more on the posterior surface of the heart, and the **right ventricle** lies below and to the right and more on the anterior surface (fig. 18).

The incisura cordis may be so deep that the apex appears doubled; this occurred in 3 of TANDLER's 300 cases and in 4 of ABBOTT's 631 cases. It is not so infrequent in the child, and is the normal character in the early fœtus, being obliterated about the 12 mm. stage (see MALL). It is a characteristic feature of the heart in Cetacea and Sirenia, being most marked in the dugong, and is also found in the Indian elephant [but see EICKER, *Anat. Record*, vol. vi.].

[1] There is often a well-defined edge to be seen between the lower parts of these surfaces: it continues the margin of the diaphragmatic surface.

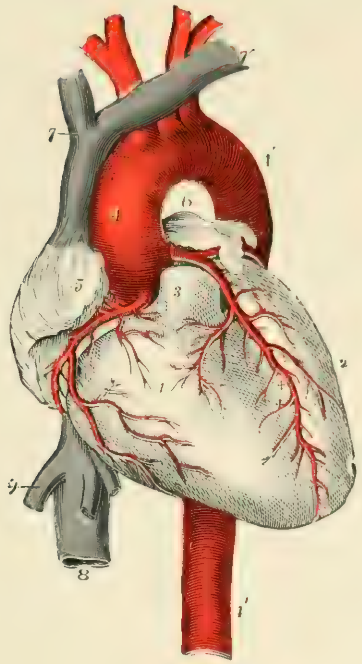


FIG. 18.—THE HEART AND GREAT SYSTEMIC VESSELS FROM BEFORE. (R. QUAIN.) $\frac{1}{3}$.

The pulmonary artery has been cut short close to its origin in order to show the first part of the aorta. 1, right ventricle; 2, left ventricle; 3, root of pulmonary artery; 4, arch of aorta; 5, right, and 6, left auricular appendage; 7, superior vena cava; 8, inferior vena cava.

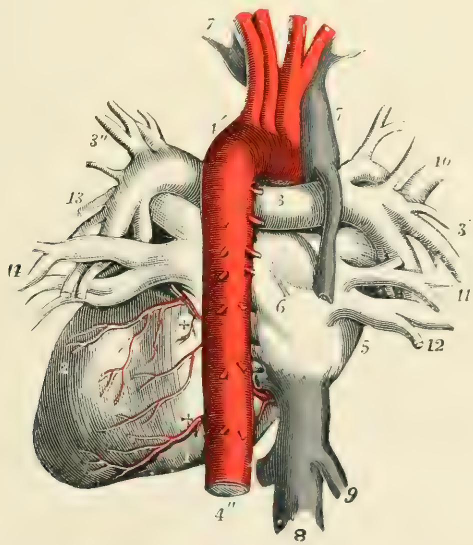


FIG. 19.—THE HEART AND GREAT VESSELS FROM BEHIND. (R. QUAIN.) $\frac{1}{3}$.

1, right, 2, left ventricle; 3, right pulmonary artery near the division of the main trunk; 5, right atrium; 7, superior vena cava; 8, inferior vena cava; 10 to 14, pulmonary veins.

[*To face page* 22.

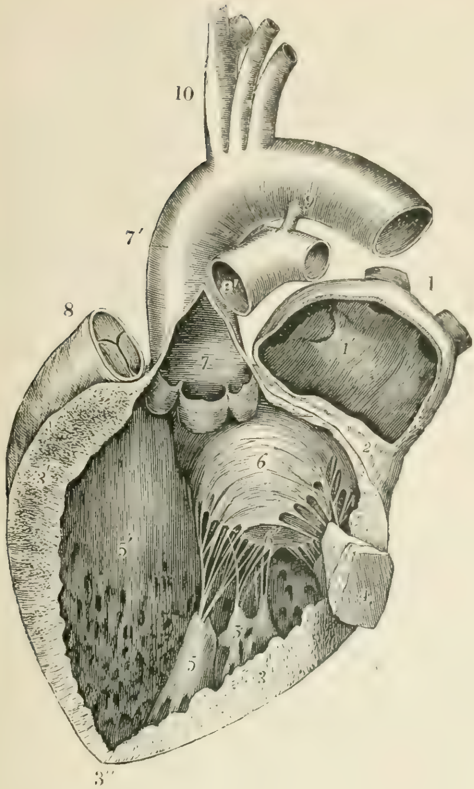


FIG. 20A.—THE LEFT ATRIUM AND VENTRICLE OPENED SO AS TO SHOW THEIR INTERIOR. (ALLEN THOMSON.)

The commencement of the pulmonary artery has been cut away, so as to show the origin of the aorta from the front of the left ventricle; part of the atrium with its appendix has been removed, and it is seen to be continuous with and to open into the back part of the ventricle. 1, right pulmonary veins cut short; 1′, placed within the cavity of the atrium on the left side of the septum, on the part formed by the valve of the foramen ovale, of which the crescentic border is seen; 2′, a narrow portion of the wall of the atrium and ventricle preserved around the atrio-ventricular orifice; 3, 3′, cut surface of the wall of the ventricle, seen to become very much thinner towards 3″, at the apex; 4, a small part of the wall of the left ventricle which has been preserved with the anterior papillary muscle attached to it; 5, 5, posterior papillary muscles; 5′, the left side of the ventricular septum; 6, the anterior or aortic segment, and 6′, the posterior or parietal segment of the mitral valve; 7, placed in the interior of the aorta near its commencement and above its valve; 7′, the exterior of the great aortic sinus; 8, the upper part of the conus arteriosus with the root of the pulmonary artery and its valve; 8′, the separated portion of the pulmonary trunk remaining attached to the aorta by 9, the ligamentum arteriosum; 10, the arteries arising from the aortic arch.

The **right ventricle** thus forms the chief part of the sterno-costal surface and a small part of the diaphragmatic surface, and, between these surfaces, the margo acutus or inferior border of the heart almost but not quite as far as the apex. It is triangular in shape when viewed from the front. Its upper and left angle

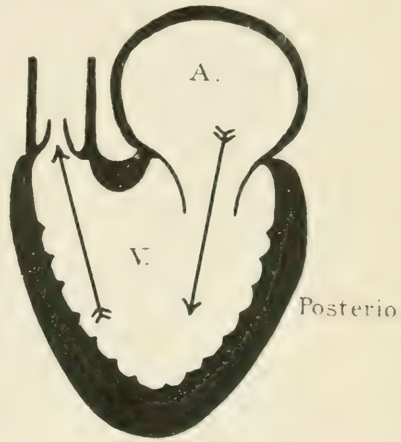


FIG. 20B.—THE RIGHT ATRIUM AND VENTRICLE IN DIAGRAMMATIC SECTION.

A., atrium; V., ventricle. The arrows indicate what may be called the "inflowing" and "outflowing" parts of the ventricle.

is prolonged above the coronary sulcus in a conical form to the commencement of the pulmonary artery. This is the most prominently arched part of the ventricle and is named the **conus arteriosus** or **infundibulum**.

The **left ventricle** forms the "left surface" (margo obtusus) of the heart, a small part of the anterior surface, and the greater part of the diaphragmatic surface. The origin of the systemic aorta from the base of the ventricle cannot be seen without dissection; in the undissected heart it appears on the right side of the pulmonary artery, its lower part overlapped by the right auricular appendix (fig. 18).

The **atrial portion** of the heart is cuboidal in form, its long axis lying transversely and curved with the concavity forwards. It forms the base of the heart and the upper part of the sterno-costal surface (fig. 17). The base on the whole is flat, though somewhat concave from side to side, and is irregularly quadrilateral in form; it is limited below by the coronary sulcus. On it there are the openings of the superior and inferior venæ cavæ, which open into the right atrium, and of the four pulmonary veins, which open into the left atrium (fig. 19). The separation of the two atria is indicated on the basal surface by an **inter-atrial groove**, usually quite distinct; it runs vertically immediately to the right of the openings of the right pulmonary veins, between them and the caval orifices, and extends as high as the opening of the superior vena cava. The sterno-costal surface of the atria is markedly concave forwards, and lying in the anterior hollow there are the pulmonary artery and the systemic aorta (fig. 23). Each atrium is continued anteriorly into an **auricular appendix** or **auricle** (auricula), and these parts curve forwards and embrace the two great arteries (fig. 23).

The **right atrium** occupies the right portion of the base of the heart and the upper and right part of the sterno-costal surface; and the rounded, convex lateral margin between these surfaces forms the **right border** of the heart (fig. 18). It is of a quadrangular form, the vertical diameter (between the venæ cavæ) being greater than the transverse diameter. The superior and inferior venæ cavæ open into it at, respectively, the upper and lower posterior angles, while the auricular appendix, a tongue-shaped part, projects forwards from the upper anterior angle and turns to the left over the root of the aorta.[1] The main part of the atrium is that into which the two great veins pour their blood; it is commonly named the **sinus venarum**. On the right or lateral wall of the atrium, and most apparent on the distended heart, there is a slight groove, often, however, only indifferently marked, the **sulcus terminalis** (of HIS), which runs from the front of the opening of the superior cava to the right side of the opening of the inferior cava; it forms the right boundary of the sinus venarum and marks it off from the atrium proper. The sinus area, then, on the surface of the heart, is bounded by the interatrial sulcus behind and the sulcus terminalis on the right. The lower and posterior part of the atrial area, close to and on the right side of the sulcus terminalis, is often dilated and then overhangs the coronary sulcus; this dilatation has been named the appendix auricularis posterior (HIS) and the sub-Eustachian sinus (KEITH), its position being below and lateral to the Eustachian valve.

The **left atrium** occupies the left portion of the base of the heart and hardly any of it, except its appendix, is to be seen from the front unless the pulmonary artery and the aorta, which are in contact with it, are cut away (fig. 23). It receives, on its posterior surface, two pulmonary veins on each side, those from the left lung entering very close together (see p. 35); on the right, on account of its transverse expansion, it often overlaps the right atrium from behind. The auricular appendix extends forwards from the left side of the atrium and, overlapping the coronary sulcus, curves towards the right side resting on the pulmonary artery. It is more curved as well as longer and narrower than the appendix of

[1] The bifurcation of the right auricular appendix, which was stated by OWEN to be a constant and specific marsupial character, has been shown by CUNNINGHAM and M'CLURE to be not uncommon in the hearts of higher mammals; "the free edge becomes notched as a result of its proximity to the root of the aorta" (M'CLURE). In seals the right appendix is very long and reaches the root of the pulmonary artery.

the right atrium and its margins are more deeply indented and sacculated;[1] and between it and the atrium there is a deep vertical cleft.

The **external form** of the heart does not vary much, even when there is a considerable departure from the normal arrangements in the interior; if these are excessive, however, the external form will reflect them. The apex of the heart, as already pointed out (p. 22), is occasionally bifid.

The heart may be **transposed** from the left to the right side of the body; usually this is associated with a general transposition of the viscera and with a right aortic arch.

There are two classical accounts of **duplication** of the heart (two hearts) in the human subject (BOERHAVE and MECKEL). It is difficult to account for these cases unless they be instances of pseudo-duplication, the second heart being a herniated piece of liver with a cavernous structure, as has been described in the rabbit by THOMPSON (*Proc. Anat. Soc.*, p. 16; *Jour. Anat.*, vol. xxxv.).

The heart and parts of the great vessels which lie within the pericardium are covered by a thin transparent membrane, the **epicardium**. This layer represents the visceral layer of the serous pericardium, which is continued on to the heart from the parietal layer at the attachments of the great vessels to the pericardium (see p. 132). The epicardium is attached to the surface of the heart by a layer of **subepicardial tissue** of very varying thickness, which is directly continuous with the interstitial fibrous tissue of the myocardium. In

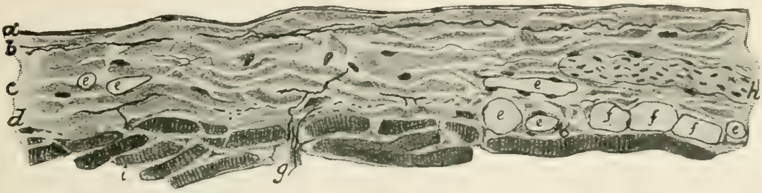


FIG. 21.—SECTION OF THE EPICARDIUM OVER THE LEFT VENTRICLE. (MANN.)

a, superficial endothelium; *b*, elastic fibres; *c*, lamina propria; *e*, blood vessels; *f*, fat cells; *h*, a small nerve; *i*, myocardium.

it, in the coronary sulcus and the interventricular grooves, there lie the coronary vessels and the nerves of the heart, before they dip into the muscle substance, and a system of lymphatic vessels connected with those of the myocardium; and there is developed in it usually a considerable amount of fat in which these structures are embedded.

The fat is in greatest amount on the ventricular border of the coronary sulcus, along the margo acutus, and in the anterior and posterior interventricular furrows, that is, along the course of the main vessels; and from these positions it extends in strips over the surface of the heart which it may entirely cover.

The **epicardium** has the usual structure of a serous membrane. It is covered externally by a layer of endothelium of irregularly polygonal cells, the height of which is greater in the contracted than in the relaxed heart (SOULIÉ). Stomata are to be found between the cells (SKWARTZOFF). The substance of the membrane (lamina propria) is composed of connective tissue in which there is a considerable amount of elastic tissue, collected chiefly in a network in the deeper layers. The elastic tissue of the atrial epicardium is continued into the elastic tissue of the adventitia of the veins, but that of the ventricular epicardium is not continued into that of the adventitia of the aortæ (SEIPP).

The epicardium appears more transparent over the ventricles than over the

[1] WINSLOW (1747) compares it to a cockscomb. It varies considerably in its length.

atria, but this is due to the deeper colour of the ventricular myocardium. In inflammatory states the epicardium may become perfectly opaque.

The amount and the extent of the subepicardial fat vary greatly in different individuals. The fat begins to be present shortly after birth (in the second month, W. MÜLLER) and increases continuously till old age, and according to MÜLLER the amount is determined by the same causes as determine the amount of the general body fat. MÜLLER further states that with an equal development of the subcutaneous fat the amount of the subepicardial fat is greater in the male than in the female. If the amount of the fat is very great it accumulates in the furrows and along the margo acutus in fissured masses and may extend as a layer over the greater part of the heart, being in smallest quantity on the basal and diaphragmatic surfaces; and in such conditions it may also be found in the larger interspaces of the myocardium and even beneath the endocardium. A semicircular fold of fat (repli préaortique, TESTUT; plica semilunaris, RINDFLEISCH) round the front of the aorta at the upper margin of the right auricular appendix is almost always to be found, especially in old people in whom it is present even when the rest of the fat is small in amount. Another fold which ascends from the coronary sulcus along the right side of the conus arteriosus has been named the plica infundibularis; but the configuration of the fat in the coronary sulcus and neighbouring parts must be greatly influenced by the form and position of the auricular appendages.

THE INTERIOR OF THE HEART[1]

The whole inner surface of the heart, and the papillary muscles, the chordæ tendineæ, and the cardiac valves, are covered with a layer of **endocardium**,[2] which gives to them their smooth and glistening appearance. On its free surface the endocardium carries an endothelial layer, and, functionally at least, it is the equivalent of the tunica intima of the blood-vessel wall. It varies considerably in thickness in different parts of the heart, but, in a general way, may be said to be inversely proportional to the thickness of the underlying myocardium; it is, therefore, thicker (four to five times, V. EBNER) in the atria than in the ventricles. It becomes very much thicker in the atria in old age and may even be thicker than the myocardium. Where it is specially thick it is white and opaque, but where it is thin the colour of the muscle is seen through it. It is most easily removed where it is thickest.

The **endocardium** increases very much (about four times) in thickness from the time of birth until adult age. In the adult it is fairly uniform in its thickness (·25 mm.) in the left atrium, but in the right atrium it is irregularly thick, being thicker at the free border of the annulus ovalis, near the torus Loweri, in the sinus region and at the mouths of the great veins, and thinner over the septum and the musculi pectinati. In the ventricles it is much thicker in the "outflowing" than in the "inflowing" parts, and this difference is more marked in the left than in the right ventricle; but thick and thin areas are often to be seen scattered irregularly over the ventricular walls, sometimes passing gradually into one another but sometimes sharply demarcated. On the left side of the ventricular septum the endocardium almost always shows

[1] The methods of opening the heart are described in text books of practical anatomy; special dissections are described by VERNEL, *Anat. Anz.*, Bd. lx., 1926.

[2] It is only comparatively recently that the endocardium has been considered a separate layer of the heart wall. Attention was first specially directed to it in the study of endocarditic affections, and it is generally agreed that BOUILLAUD, in his descriptions of endocarditis, in 1835, was the first to use the term endocardium.

longitudinal white markings, which only in small part belong to the ramifications of the atrio-ventricular system (see p. 83). On the trabeculæ and the papillary muscles the endocardium is very thin; on the former it is thicker on the surface facing the cavity of the ventricle and on the latter on the surface facing the " outflowing " part of the chamber.

The endocardium appears never to be thrown into folds in any phase of cardiac contraction, a circumstance due to the large amount of elastic tissue it contains. This tissue is said to be stretched in diastole and to be in its rest phase in the systolic heart (TANDLER).

Microscopic Structure.—The structure of the endocardium varies at different parts of the heart, and this may well account, in part at least, for the different number of layers which have been described in it by different authors. In general, however, it may be said to consist of three layers, (*a*) an endothelial layer, (*b*) a membrana propria, and (*c*) a subendocardial layer.

(*a*) The **endothelial layer** consists of a single stratum of characteristic endothelial cells, which are, however, more isodiametric than the corresponding cells of the blood-vessel wall.

(*b*) The **membrana propria** shows considerable variation in its structure at different parts. Next to the endothelium there is a loose layer of delicate fibrillar tissue, the subendothelial layers of some writers (KÖNIGER, MANN), and external to this a stronger connective tissue layer which contains a considerable amount of elastic tissue. In the inner part of this layer the elastic fibres form membranes, which resemble the elastic membranes of the aorta on the atrial wall close to the atrio-ventricular orifice, and the internal elastic membrane of a medium-sized blood

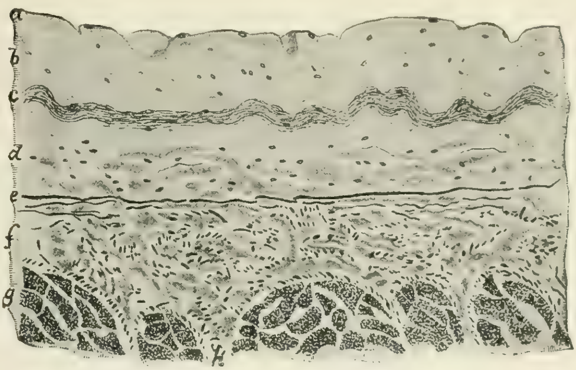


FIG. 22.—ENDOCARDIUM OF RIGHT ATRIUM. (MANN.)

a, endothelial layer; *b*, layer of loose fibrous tissue; *c* and *e*, elastic tissue; *d*, coarser fibrous tissue; *f*, subendocardial layer; *g*, myocardium.

vessel in the upper parts of the ventricles (LUSCHKA, SEIPP, V. EBNER); while in the outer part of the layer the elastic fibres are coarser and are not grouped together. There are also to be found in the membrana propria non-striped muscle fibres, as was first pointed out by SCHWIEGGER-SEIDEL, and afterwards confirmed by RANVIER, ALBRECHT, RENAUD, and NAGAYO. They generally lie in the outer fibrous tissue, but may extend into the inner layer. They are most abundant in the " outflowing " part of the left ventricle, especially on the smooth part of the septal wall and on the surface of the papillary muscles which face into this cavity; they are less abundant under the pulmonary orifice and in the atria, and according to KÖNIGER there are a few fibres in the atrio-ventricular valves. (The smooth muscle is large in amount in the reptilian heart; see SHANER, *Anat. Record*, vol. xxv.) Both elastic and muscle fibres are absent during fœtal life. At birth the elastic fibres have been said to be very sparse and the smooth muscle fibres hardly to be recognised (NAGAYO), but MILLER and PERKINS (*Amer. Jour. Anat.*, vol. xxxix., 1927) have demonstrated a considerable amount of elastic tissue in the heart of an infant two days old; but this tissue undoubtedly increases during life and is very markedly increased in amount in old age.

(*c*) The **subendocardial layer** attaches the membrana propria to the underlying tissues. It consists chiefly of fibrous tissue in which scattered coarse elastic fibres are present; and adipose tissue is also frequently found in it. The terminal ramifications of the atrio-ventricular bundle lie in this layer and it carries also a vascular network, the membrana propria being avascular; LANGER, however, considers these vessels to be the vessels of the unstriped musculature (see p. 46).

The question of the **homology of the endocardium** and the layers of the peripheral blood-vessel wall cannot be said to be decided. The older view is that the endocardium corresponds

to the tunica intima of the vessel wall, but the view, first stated by LUSCHKA, that it corresponds to the whole thickness of the vessel wall, and that the myocardium is an additional mantle not represented in the vessel, has now received considerable support (NAGAYO, KOCH, MANN). The difficulties of this latter homology, however, especially at the arterial orifices (see p. 49), have been frequently pointed out (KÖLLIKER, SEIPP), and a third view, that the endocardium corresponds to the intima and media and that the adventitia is represented by the fibrous tissues of the myocardium and of the subendocardial and subepicardial layers and contains the myocardium, has been advanced by TANDLER. The older view, it must be admitted, is expressed entirely on a functional basis. It must also be admitted, however, that it is not possible directly to follow the individual layers of the vessel wall on to so modified a part of the system as the heart, or even to hold that an apparent continuity is evidence of an homology. LUSCHKA sought to establish his view by showing that the atrial endocardium is continuous with the whole wall of the entering veins, the subendocardial layer (?) being homologous with the adventitia. SEIPP, in his studies of the elastic tissue of the heart, showed that the elastic tissues of the aorta and pulmonary artery originate quite independently of those of the heart and that the presence of the fibrous rings at the orifices precludes any continuity between them. An appeal to the developmental history of the parts seems to define the problem best. On this basis a strict homology may be established between the endothelial layers, and it can only further be stated that

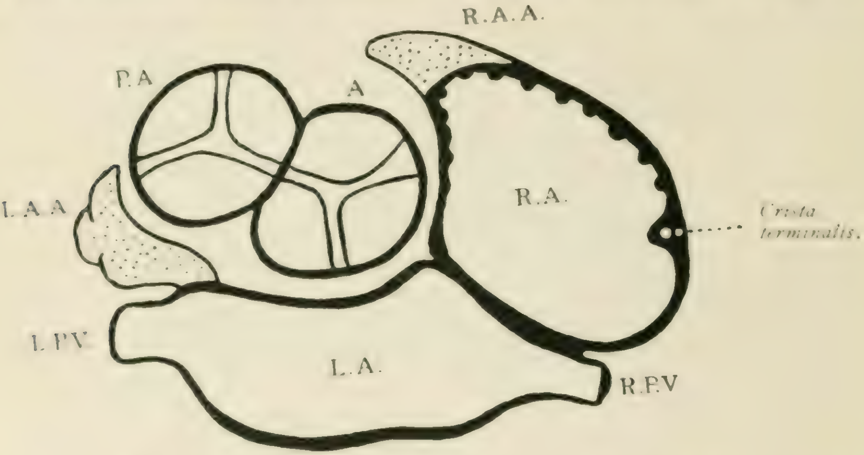


FIG. 23.—DIAGRAM OF A TRANSVERSE SECTION THROUGH THE ATRIA.
L.A.A., R.A.A., left and right auricular appendages; P.A., pulmonary artery; A., aorta; L.P.V., R.P.V., left and right pulmonary veins.

while the remainder of the heart wall may be derived from the myo-epicardial mantle of splanchnic mesoderm the remainder of the vessel wall is probably derived from the surrounding mesoderm. A fuller statement can be made only when the origin of the fibrous tissue and muscular elements of the endocardium, either from the endothelium or from the myo-epicardial mantle, is definitely established.

The features of the interior of the four chambers of the heart are so different that each of them requires to be described separately; but to appreciate the relations of each chamber to its fellow of the opposite side and to understand the names which are given to its different walls, it is an advantage to study first transverse sections of the heart through the atria and through the ventricles.[1]

The Atria.—A transverse section through the **atria** (fig. 23) shows their general convexity forwards and the flattened dorsal wall; and demonstrates that the septum which separates them is obliquely placed, running from in front backwards and to the right. The left atrium, cuboidal in form, lies behind the pulmonary artery and the aorta; it forms much more of the base of the heart

[1] For convenience of description the heart is now supposed to be in its conventional position, that is to be placed vertically with the apex downwards.

than does the right atrium. The posterior wall of the right atrium is narrow and at the crista terminalis is continued into the lateral or right wall. The anterior walls of the two atria meet one another and are continued into the septum at a definite angle which, placed as it is behind the aorta, may be named the aortic angle (KEITH). In the floor of each atrium lies the atrio-ventricular orifice (fig. 20).

Right Atrium.—The cavity of the right atrium is of an irregular quadrilateral form. Its longest axis lies between the openings of the superior and inferior venæ

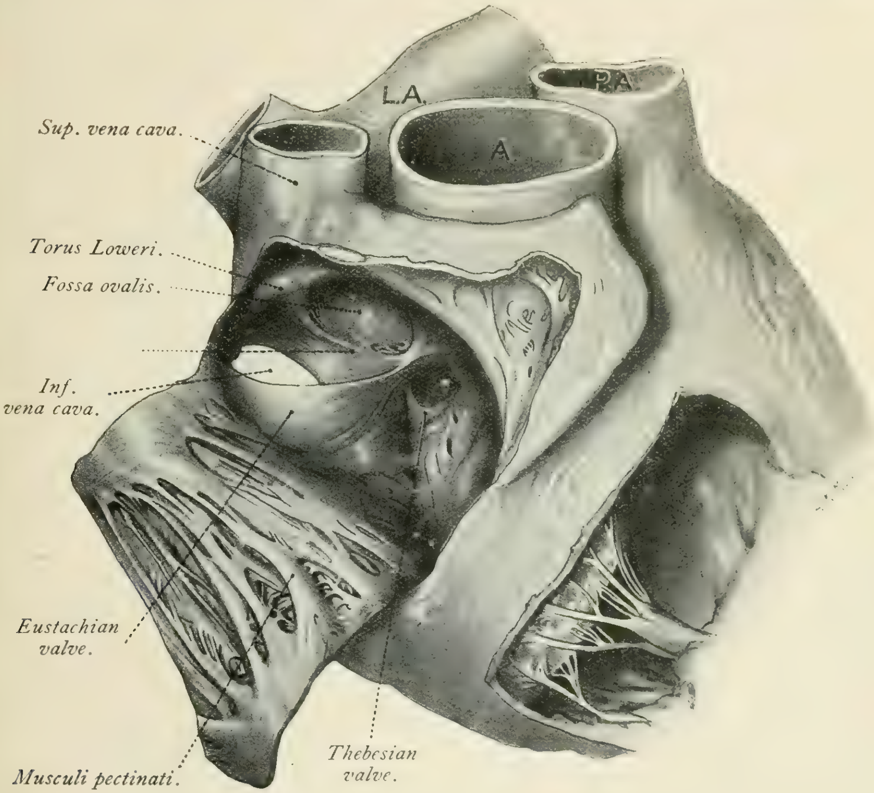


FIG. 24.—DISSECTION OF THE RIGHT ATRIUM. (Drawn by A. K. MAXWELL.) The crista terminalis is shown cut in front of the left edge of the superior vena cava.

cavæ and is vertically placed, running from above downwards in the normal position of the heart (fig. 19). The posterior and the medial (or septal) walls present a smooth and even surface, and in the part of the cavity which they bound, the **sinus venarum** part of the atrium, there are seen the openings of the superior and inferior venæ cavæ, the former directed downwards and forwards and the latter, larger [1] and placed a little further back, directed upwards and forwards. The sinus part of the atrium is limited on the right side by a vertical muscular ridge, the **crista terminalis**, which corresponds in position to the sulcus terminalis on the external surface. The smoothness of this part of the atrium is distinctive, for almost the whole of the rest of the interior, the atrium proper, is ridged with parallel

[1] The diameter of the superior cava is 18 to 22 mm., and of the inferior cava 27 to 36 mm.

elevations between which there are narrow deep depressions. The elevations are produced by muscle bundles named the **musculi pectinati**. They spring from the crista terminalis and run forwards at right angles from it. On the lateral (or right) wall of the atrium they lie horizontally and parallel and there are few junctions between them, but further forwards they are more vertical in direction and the connections between the columns so increase that a muscular network is formed. This network reaches its greatest complexity in the auricular appendix, the musculi forming there a closely set reticulum, the larger trabeculæ of which are vertical; and, towards its apex, some of the bands free themselves from the wall and pass across the cavity. The general direction of the musculi is towards the atrio-ventricular orifice near which they terminate rather suddenly, usually after dividing into smaller bands; and sometimes they appear to end in a semi-circular ridge which lies about ¼ in. above the margin of the orifice. Musculi pectinati are absent in the neighbourhood of the atrio-ventricular orifice; they are also absent in the sub-Eustachian diverticulum.

The **tænia sagittalis** is the name given to a prominent muscle band which arises from the crista terminalis near the left side of the superior cava and passes forwards over the roof of the atrium. If it represents, as is commonly held, the septum spurium (p. 39), then the septal part of the crista terminalis belongs to the left venous valve.

The **crista terminalis** begins on the upper part of the medial (septal) wall, and from its origin arches from the medial to the lateral side in front of the orifice of the superior vena cava, which thus comes to have a definite sharp border in front and on the right side (fig. 26). The crista then follows an arched course on the posterior wall, near its junction with the lateral wall (fig. 23) along the anterior margin of the sulcus terminalis (p. 24), and ends by dividing into a number (three to six) of smaller bands which are continued towards the atrio-ventricular orifice and end on the lateral side of the posterior part of the Eustachian valve. The crista is formed by a large, well-defined muscle bundle, the description of which is given with the heart musculature (p. 72).

The atrial wall behind the crista terminalis is, as already stated, perfectly smooth. It is continued upwards and downwards into the posterior walls of the upper and lower cavæ, there being no definition on the surface of the transition from the atrium to the veins. The part of the atrial wall between the two caval orifices is convex towards the atrial cavity, the height of the convexity forming a rounded, horizontally placed ridge, which is named the **intervenous tubercle** (or **torus**) of **Lower** (tuberculum intervenosum, Loweri) (fig. 24).

Very great differences of opinion have been expressed on the form and even of the existence of this tubercle. LOWER himself (1669) describes it as follows: "Itaque ante limen auriculæ dextræ nempe eo loci ubi vena cava ascendens cum descendente congressa alveum suum in auriculam [illegible] parietis est, tuberculum quoddam a subjecta pinguedine elatum et notatu valde dignum occurrit, cujus obtentu sanguis per venam descendentem delapsus in auriculam divertitur, qui alioquin in venam ascendentem decumbens sanguinem per istam cor versus assurgentem reprimeret valde et retardaret." HALLER completely denies the existence of the tubercle and CRUVEILHIER, SAPPEY, and especially POIRIER, also deny its presence. RETZIUS has pointed out that the diagrams given by LOWER do not correspond to the usual findings, but he supports LOWER's general statements and physiological deductions. According to [illegible] the so-called tubercle of Lower is a necessary consequence of the direction of the two caval blood streams and not an independent formation; while concerning it HENLE says: "Hinter der Oeffnung der Vena cava superior folgt der quere, an der äusseren Fläche durch eine Einbiegung angedeutete Wulst, Tuberculum (Loweri), der sich wie ein scharfkantiger Wall zwischen den Mündungen der beiden Hohlveven erhebt und die aus beiden Mündungen kommenden Ströme abzuweisen dient. Ein durch die Diche der oberen Wand des Atriums senkrecht auf diesen Wulst geführter Durchschnitt zeigt, dass derselbe seine Form einer Einlagerung von Fett verdankt, welches zwie Schnichten der Musculatur von einander scheidet, von denen die

eine der Einbeigung folgt, während die andere über dieselbe hinwegzieht." HYRTL admits the existence of the tubercle in the embryo, but in the adult it appears to him to be so indeterminate that it is not easily recognised. According to TOLDT the tubercle is formed because the right atrium is bent round the left atrium in the same manner in which the right ventricle is bent round the left ventricle.

Without further discussion, while it must be admitted that the illustration given by LOWER does not express the actual conditions, for there is shown by him a great thorn-like process,[1] it may be said that a tubercle, most frequently appearing, as described above, in the form of a transverse rounded ridge, is always to be found in the well-fixed heart, but may not be observed in the flaccid unfixed heart removed for post-mortem examination. It can be more readily recognised if it be remembered that the axes of the two caval blood streams (in the fœtus even more than in the adult) are not in the same straight line, but form with one another an angle

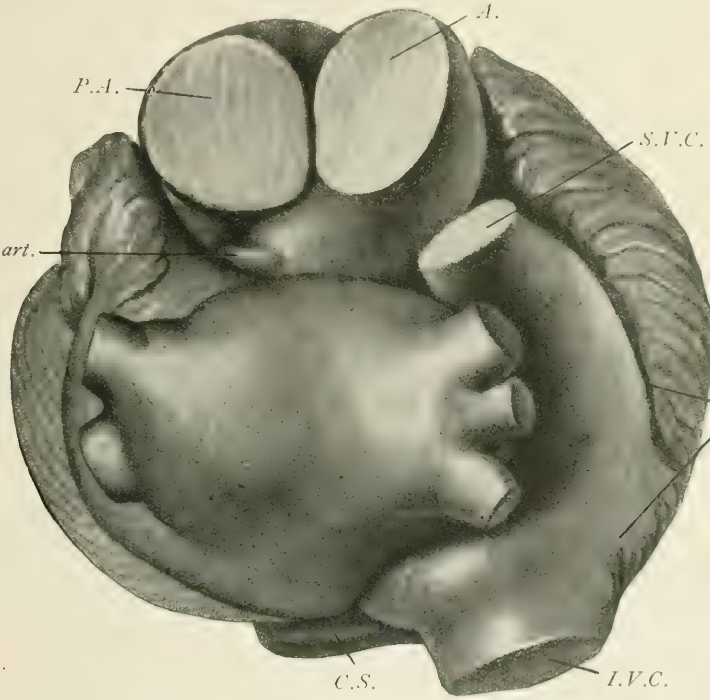


FIG. 25.—CAST OF THE INTERIOR OF THE HEART VIEWED FROM THE POSTERIOR SURFACE. ($\frac{5}{6}$ net size. From Tandler's "Anatomie des Herzens" (GUSTAV FISCHER, Jena).)

The form of the right and left atria is shown. There are three right pulmonary veins in this heart. P.A., pulmonary artery; A., aorta; S.C.V., superior vena cava; C.T., crista terminalis; I.V.C., inferior vena cava; C.S., coronary sinus.

open backwards. Because of this angulation there normally will be a forward convexity of the posterior sinus wall between the two caval openings. That this angulation is in reality the normal form may be shown in the following way (TANDLER): If a heart enclosed in the pericardium be removed from the body and the pericardium opened from the right, the angular position of the two venæ cavæ to one another in the unfilled heart will be seen; and it will not be possible to obliterate this angle by pulling on the two cavæ, on account of the pericardium which extends from the entrance of the upper to the entrance of the lower vein. If this piece of pericardium [2] be cut through the angle may be readily obliterated. The tubercle of Lower, however, is more than the mere expression of the apex of this angle, towards which the two caval

[1] The heart figured by LOWER is almost certainly not a human heart; it is probably that of a dog.

[2] This piece of pericardium will transmit the pull of the diaphragm from the inferior caval orifice to the superior cava and the root of the lung.

blood streams run, for, as will be described more fully later, there is to be found here a variably developed muscle bundle which runs laterally from the atrial septum to the crista terminalis and forms the basis of the tubercle (p. 72). KEITH has fully described this muscle band and pointed out its importance. Since the tubercle is not a tubercular elevation as described by LOWER, but more frequently is a transversely running ridge, it has been suggested that the name "torus" should be used for it (TANDLER). The fatty pad described by HENLE can be recognised in section microscopically and it will be seen that it lies not only on the surface of the atrium but actually in the atrial wall, so that one layer of musculature lies dorsal and another ventral to it.

In most pronograde mammals the ridge-like torus is very much more strongly developed than in man, without there necessarily being any increase in the angle of convergence of the two venæ cavæ [1] and in these instances there is a much more strongly developed band of muscle. The ridge is most strongly developed in the heart of the seal, in which it forms almost a septum between the openings of the two cavæ. The condition in the horse is somewhat similar, and in the dog it is well developed.

The orifice of the **superior vena cava** is oval in shape and very oblique in the normal position of the heart, the lateral end being much lower than the medial end. The anterior margin of the orifice is formed by the crista terminalis and the indefinite medial margin largely by the septum; the posterior and lateral walls of the vein are continued into the atrial wall. In rare cases the orifice is flanked laterally and in front by a valve, a persistent upper part of the right venous valve (TURNER, *Jour. Anat.*, vol. iii.; JOHNSTON, *ibid.*, vol. xlix.). The orifice of the **inferior vena cava** is oval in shape and obliquely placed, the lateral end being higher than the medial end. Its posterior wall is formed by the septum and is continued into the floor of the fossa ovalis, while it is flanked in front and partly covered by a semilunar fold, the **Eustachian valve** or the valve of the inferior vena cava (valvula venæ cavæ inferioris) (fig. 24). This structure, a rudiment of the right sinus valve of the heart of the embryo, is of very great variability in its size and form. Its convex border is continuous with the anterior margin of the caval orifice, and from there it is prolonged in front into the anterior limb of the limbus fossæ ovalis and behind on to the posterior wall of the atrium in the groove which lies between the inferior vena cava and the sub-Eustachian diverticulum. In the fœtal heart, its free, concave, cranial border is directed upwards and medially, and it is then of great functional significance for it directs the blood stream from the inferior vena cava towards the open foramen ovale (fig. 26). (See further, p. 33.)

The **Eustachian valve** of the adult heart, which is derived only from the basal part of that portion of the right venous valve which bounds the inferior caval orifice in front, is of varying height and in very few instances does it exceed 1 cm. Very often it is perforated and it may even present the appearance of a network or a delicate trellis. Forms in which the network has reached great complexity have been described by HALLER, GEGENBAUER, CHIARI, and LAMBERTZ; and CHIARI has described similar retrogressions of the right venous valve and the septum spurium in a case of malformation of the heart. Network formations on the lower part of the fossa ovalis, medial to the opening of the inferior vena cava, have been frequently described (LOWER, WEBER, CHIARI, OPPENHEIMER); they consist of rudiments of the left venous valve; and those described by WEBER, in the form of a network at the posterior border of the fossa ovalis, medial to the orifice of the superior cava, are also very frequently to be found. Between this network and the septum a small slit-like space may exist which WEBER believes to be the remains of the spatium interseptovalvulare (p. 40). Wider reticular formations, extending across the cavity of the atrium from the crista terminalis to the septum and including below the Eustachian valve, have also been described (MONTEIRO, *Jour. Anat.*, vol. lii., 1917); they represent more extensive persistences of the venous valves. Fine isolated muscle fibres are

---

[1] The convergence of the cavæ to one another is, however, usually greater; in man and the anthropoids the angle is about 140°, in many other mammals about 100°, and it is about the [illegible]

often found in the Eustachian valve (TANDLER). There is little variation of the Eustachian valve in the fœtus, a circumstance which corresponds with its importance in the fœtal heart. It is not implied, however, in this description, that the whole of the inferior caval blood passes through the foramen ovale or that none of the superior caval blood does so; the experiments of POHLMAN on the fœtal circulation indicate that there is considerable mixing of the two streams and that a mixture passes through the foramen (see also KELLOG, *Anat. Record*, vol. xxxv.). At or soon after birth the free non-muscular part of the valve undergoes retrogressive changes. If the Eustachian valve be pulled on laterally there will be raised on the medial wall of the atrium, as a continuation of the free border of the valve, a thin sharply defined fold, directed longitudinally upwards towards the torus aorticus (see p. 35). This fold is formed

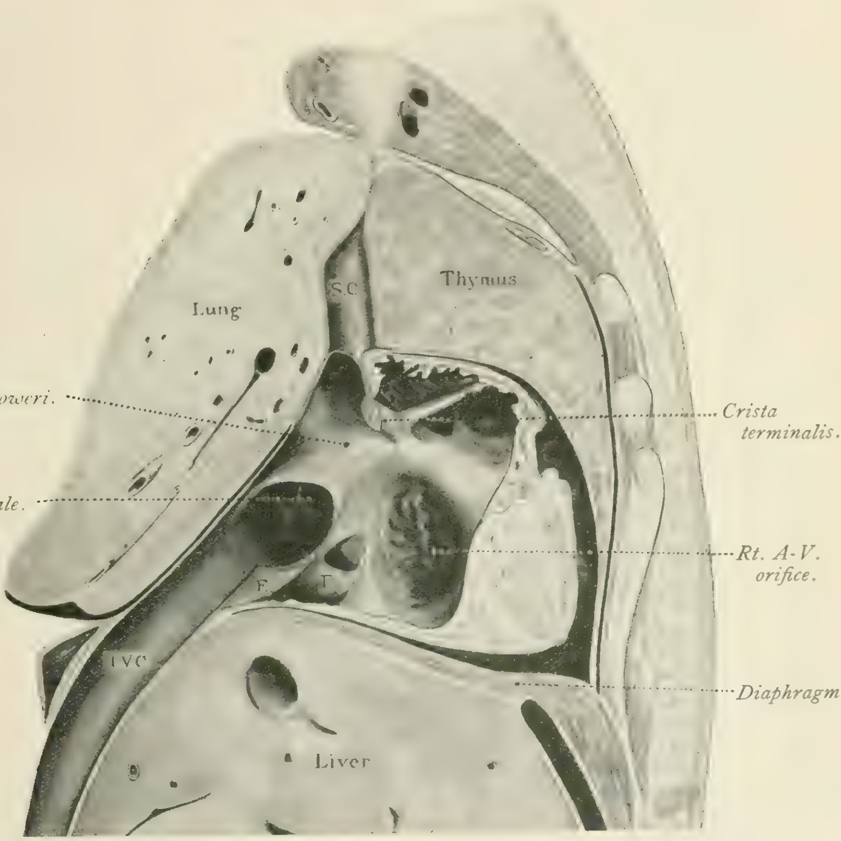


FIG. 26.—SAGITTAL SECTION OF THE THORAX OF A FULL-TERM FŒTUS.
The surface of the left half is viewed.

E., Eustachian valve; T., Thebesian valve; I.V.C., inferior vena cava; S.C., superior vena cava.

by a flat glistening fibrous-tissue band, at the most about 1 mm. broad; it was described by TAWARA in 1885, but is now usually named, after French writers, the **tendon of Todaro.** Near the valve, in the fibrous tissue of which it spreads out and ends, this band lies immediately under the endocardium and may be seen through it as a grey strip; in its course in the atrial wall it becomes more and more covered by atrial muscle, but is easily traced to its origin in the right trigonum fibrosum.

At the junction of the floor of the atrium with the medial (septal) wall and just in front of the anterior end of the Eustachian valve, there is to be seen the circular opening of the **coronary sinus.** It is flanked laterally by the **Thebesian**

valve,[1] or valve of the coronary sinus (valvula sinus coronarii) (fig. 24), which is very variable in its size and form. Most commonly it is smaller than the coronary opening and is semilunar in shape, its free concave margin being directed upwards and medially towards the atrial septum; but very frequently it is perforated or in the form of a network, and occasionally it exists only as a few delicate filaments attached to the lateral surface of the Eustachian valve and bridging across the sub-Eustachian diverticulum. It is derived with the Eustachian valve from a common part of the right sinus valve, and not infrequently the two remain closely connected together.

The **Thebesian valve** has been seen doubled. The opening of the coronary sinus is sometimes on the bottom of a small fossa. The sub-Eustachian diverticulum (see p. 24) is the pouch which lies between the lateral surface of the Eustachian valve and the posterior wall of the atrium (fig. 24). It has been aptly compared by KEITH to the sinuses of Valsalva, for when the atrium contracts it is distended and presses the Eustachian valve backwards, and so assists in the closure of the inferior caval orifice. The coronary sinus may open into it if the Thebesian valve be very deficient. The atrial wall of the diverticulum is thin and translucent.

The **atrio-ventricular orifice**, oval in shape, also lies in the floor of the atrium, but in the normal position of the heart in the thorax the plane of the opening is nearly vertical and it lies in the medial and anterior part of the cavity (fig. 26). It is guarded by the **tricuspid valve**, which is described on p. 53.

The area of the atrial wall which lies just above the atrio-ventricular opening, and which is bounded above by the passage of the Eustachian valve into the anterior limb of the limbus fossæ ovalis and laterally by the Thebesian valve (fig. 24), is of special interest; for in this area, as first defined by KOCH, is placed the node of Tawara (see p. 80).

The medial wall of the right atrium is formed by the inter-atrial septum (fig. 23). Its surface is devoid of musculi pectinati, but there are to be seen on it evidences of its complicated development. At its lower part, just above and a little in front of the orifice of the inferior vena cava, there is an oval depressed area, the **fossa ovalis**.[2] This part of the septum, formed from the septum primum, is thin and translucent, and contains little muscle tissue; it is often named the "pars membranacea" of the atrial septum. It is surrounded at its posterior, upper, and anterior borders by a prominent rounded fold, the **limbus fossæ ovalis** or annulus ovalis Vieussenii, which, however, is very variable in its development, in some instances being scarcely perceptible and in others being a well defined, plump, rounded band. The anterior part of the limbus is often more strongly developed, and in such cases there is usually a more or less deep pocket, directed forwards and upwards, between the upper part of the limbus and the pars membranacea, and in about 25 per cent. of all subjects there is here a slit like communication with the left atrium, which is the remains of the foramen ovale of the fœtus.

The **foramen ovale** was found to be patent in 24.2 per cent. of adult males and 29 per cent. of females; in children under one year it was patent in 94 per cent., and between one and five years in 50 per cent. ([illegible], Collect. Invest., *Journ. Anat.*, vol. xxxii.; see also SIMPSON, *Journ.*

---

[1] The valve had been previously figured by EUSTACHIUS.

[2] The fossa ovalis and limbus ovalis are wanting in monotremes and marsupials (*Perameles* being a possible exception), as the atria communicate in the embryos of these groups by a number of secondarily formed openings which close at an early stage of development in correlation with the short intra-uterine life. The conditions are similar in birds (see p. 11). (OWEN, "Marsupialia," Todd's *Cycl. Anat.*, vol. iii.; CUNNINGHAM, Chall. Reports, "Zoology," vol. v.; RÖSE, loc. cit.; PARSONS and WINDLE, "Anatomy of Macropus rufus," *Journ. Anat. and Phys.*, vol. xxxii.)

Anat., vol. xxxii.; FAWCETT and BLACHFORD, *ibid.*, vol. xxxv.; NAÑAGAS, *Anat. Record*, vol. xxi.) The most common arrangement is an oblique slit, from a pinhead size to 1 cm. in diameter, under the point of greatest convexity of the annulus. This slit may be blind, even when it leads into a diverticulum 2 cms. long, or it may open into the left atrium under the fold which is there present (p. 36). Occasionally there may be a blind slit on the left side and none on the right side; less commonly there are two blind slits.

A foramen may exist in the atrial septum above and behind the fossa ovalis; it must be due to a defect in the attachment of the septum secundum. It may be present with a persistent foramen ovale. Cases are recorded by HEPBURN, *Jour. Anat.*, vol. xxi., and GREENFIELD, *ibid.*, vol. xxiv. Deficiencies in the septum below and in front of the fossa ovalis are more common, though still comparatively rare (ARNOLD, *Virch. Arch.*, vol. li.). They represent persistences of the foramen primum. Typical cases are recorded by WARDROPP-GRIFFITH, *Jour. Anat.*, vol. xxxiii.; KEITH, *ibid.*; THOMPSON, *ibid.*, vol. xxxvii.; MORISON, *ibid.*, vol. liv. The foramen lies in front of the anterior limb of the annulus, its anterior boundary being formed by the upper parts of the aortic cusp of the mitral valve and the anterior and septal cusps of the tricuspid valve. It is often described as occurring at the site of the atrio-ventricular part of the pars membranacea septi (p. 55) (KEITH, THOMPSON), but the formation of the membranous septum, as described in this work (p. 60), precludes such an interpretation. The foramen is inter-atrial. It is usually present when the right pulmonary veins open into the superior vena cava (see p. 41); but in a specimen described by INGALLS (*Anat. Record*, vol. i.) in which the superior cava received the right pulmonary veins and opened into both atria the septum was complete. The septum is often thinner in the position of the foramen.

The **fossa ovalis** varies very much in its size, but seldom exceeds 3·5 cms. in its maximum diameter. The floor is sometimes crossed by folds of endocardium, remains of the left sinus valve, and very occasionally it is perforated in its lower part.

The **limbus** is formed by well-defined bands of atrial muscle, the superior and inferior limbic bands (KEITH, see p. 72), but in about 5 per cent. of hearts there is no trace of them; they are believed, however, to play a large part in the closure of the inferior caval orifice. The superior part of the limbus is continuous with the torus Loweri, while the antero-inferior part is usually continued into the Eustachian valve.

There is an eminence, the **torus aorticus**, on the upper and anterior part of the medial wall; it corresponds to the aorta on the external surface of the atrium (fig. 23).

There are also to be found in the right atrium the openings of three or four venæ parvæ cordis (see p. 108), and scattered over the surface there are a number of other small openings. These openings are of two kinds: (1) **Foramina of Thebesius**, at the most $\frac{1}{2}$ mm. in diameter, some of which are merely shallow recesses closed at the bottom, while others will be described later to be the mouths of small veins, the venæ minimæ cordis (p. 108); and (2) much larger openings, 2 to 3 mm. in diameter, which were first described by LANNELONGUE. They are sharply circumscribed and in their floor there are the openings of secondary foramina. These **foramina of Lannelongue** are remarkably regular in their occurrence; they lie chiefly on the medial wall, and one is usually to be found just above the upper part of the limbus fossæ ovalis and another just above the opening of the coronary sinus (fig. 24).

Left Atrium.—The form of the left atrium, as can be well seen on a cast of the cavity (fig. 25), is irregularly cuboidal. Its longest measurement lies transversely and this is emphasised, especially on the exterior, by lateral diverticula of its upper posterior parts. The pulmonary veins, two on each side and each about 14 to 15 mm. in diameter, are directed in the long axis of the cavity and open into these lateral pouches; [1] the orifices are elliptical, rather than round, with anterior and posterior margins. The two veins of one or both sides, it is to be noted, are sometimes united before they enter the atrium, while in other subjects an additional vein is found, more frequently on the right side (see p. 41).

---

[1] The left atrium is thus elongated in the direction of the axes of the pulmonary veins as the right atrium is in the axes of the superior and inferior venæ cavæ.

The surface of the cavity is smooth except in the auricular appendix, the walls of which are ridged with large numbers of musculi pectinati. The opening of the appendix, which is placed on the upper part of the anterior wall close to the left wall, is separated from the openings of the left pulmonary veins by a well-defined ridge.[1] The posterior wall of the atrium is slightly convex in the region between the pulmonary veins, the convexity being produced by the œsophagus which descends behind the atrium; on the convexity there is almost constantly a foramen of Lannelongue. There is a similar but slighter bulging, produced by the aorta, at the junction of the anterior and medial walls (fig. 23). On the medial wall, which is formed by the inter-atrial septum, there can sometimes be recognised an oval area corresponding to the fossa ovalis of the right atrium,

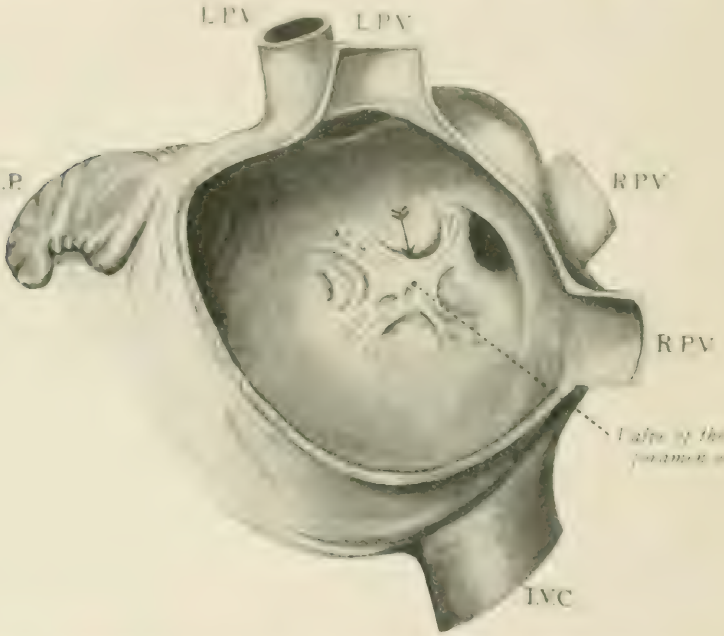


FIG. 27.—THE INTERIOR OF THE LEFT ATRIUM, SHOWING THE ATRIAL SEPTUM. The left auricular appendix, the left and right pulmonary veins, and the inferior vena cava are shown. The arrow indicates the orifice of a persistent foramen ovale.

but if it cannot be seen it can be readily defined by holding the septum to the light since it is transparent;[2] and at the upper and anterior part of this area there is to be seen the free border of the **valve of the foramen ovale** (septum primum). If the border is well developed it forms a sickle-shaped ridge, the concavity of which is directed upwards and forwards, and between this and the septum there is a deep slit-like space; but frequently there is only a faint network of fibres which radiate upwards and forwards over the fossa ovalis area and appear to be laid on the septum (fig. 27).

The **valve of the foramen ovale** was described by VETTER in 1804 as the left sinus valve, and in 1848 by PARCHAPPE as the "interauricular valve," which during fœtal life is applied to

[1] This ridge is not produced by any specially developed band of muscle, but is simply a folding of the atrial wall. It varies in its size.

[2] The thickness of the atrial septum varies at different parts from 1 to 4 mm.

the left side of the then open foramen ovale; it is, however, as is described above, the edge of the septum primum (p. 39). If a communication remains between the atria it opens into the left atrium in the concavity of the ridge. Fibrous or fibro-muscular bands, sometimes ½ in. broad, are not infrequently to be found passing from the atrial septum in the neighbourhood of the valve of the foramen across the cavity of the atrium to the anterior wall. These bands may be broad enough, though rarely so, to form a septum dividing the atrium into a postero-superior part which receives the pulmonary veins and an antero-inferior part which contains the orifice of the atrial appendix and the atrio-ventricular opening (POTTER, *Jour. Anat.*, vol. xxxix.). The condition seems to have been described first by FLOWER (*Path. Trans.*, 1882). It represents an exaggeration of the normal and may be present with or without a patent foramen ovale (cases are described by ROLLESTON, HEPBURN, WARDROPP-GRIFFITH, *Proc. Anat. Soc.*, *Jour. Anat.*, vol. xxx., and *ibid.*, vol. xxxiv. and vol. xxxvii.). It is not due to non-absorption of the sinus of the pulmonary veins, as is shown by the septum between the two atria being complete. The conditions of the foramen ovale and its valve are often peculiar in the sheep, the valve being large and having chordæ tendineæ and papillary muscles which attach it to the atrial walls; and these forms much resemble the abnormal forms found in the human subject. (See ROWLANDS, *Jour. Anat.*, vol. xxviii.)

The **atrio-ventricular orifice** lies in the floor of the atrium which, when the heart is in position in the thorax, is directed forwards and to the left. It is of an oval form and somewhat smaller than the right opening. It is guarded by the **mitral valve**. There are scattered over the surface of the left atrium numerous openings of venæ cordis minimæ.

The Development of the Atria. The **sinus venosus**, as was previously described (p. 17), consists of a transverse part and two curved lateral horns, the right of which is larger than the left (fig. 12); and it opens into the right part of the primitive atrium through an oval vertically placed opening in the dorsal wall of that chamber, the opening being flanked by the right and left venous valves (fig. 13). The lateral horns of the sinus receive at their extremities the ducts of Cuvier; and, by a series of changes which need not be described here, the inferior vena cava replaces the umbilical and vitelline veins of both sides and opens into the right end of the transverse part. In the succeeding stages of development, the left horn lags behind the right horn more and more, for the left duct of Cuvier and its tributaries no longer conduct the blood of the left side of the body to the heart; transverse connections are formed between the left and right cardinal veins and the blood of the left side passes in these connections to the right side (see Vol. I.). The left horn, with part of the transverse portion of the sinus, ultimately becomes the coronary sinus of the heart and the left duct of Cuvier becomes the oblique vein of Marshall (p. 107); for a time these parts are separated from the surface of the atrium, though attached to it by a mesenterial-like fold of pericardium, but later this fold disappears and the coronary sinus lies in contact with the atrial wall along the atrio-ventricular groove. (See further, "The Structure of the Coronary Sinus.") The right horn of the sinus is gradually absorbed into the right atrium and forms that part of this chamber which is limited on the right by the sulcus, and crista, terminalis, and in which there are the orifices of (1) the inferior vena cava; (2) the superior vena cava (the lower part of which is the right duct of Cuvier); and (3) the coronary sinus. The musculature of the sinus wall, which is never well developed, appears to be replaced by the musculature of the atrium, and there remain, as sinus musculature, only the fibres, or at least some of them, which surround the terminal part of the superior cava and those in the wall of the coronary sinus.

The parts which form the **atrial septum** and divide the primitive atrium into right and left chambers, are: (1) The **septum primum** (BORN) [1] which appears

[1] The septum primum of BORN includes the septum superius and the spina vestibuli of HIS, the latter an ingrowth from the right margin of the area interposita (HIS).

as a crescentic fold in the roof of the atrium (p. 17). It is accentuated by the enlargement of the lateral atrial diverticula, but also grows actively along the anterior and posterior walls and its free edge advances further and further into the cavity until it reaches the atrial canal from above (anteriorly) and below (posteriorly) (fig. 28). The lower edge of the septum, which is covered by a thickening of the subendocardial tissue, ultimately (about the beginning of the fifth week) fuses with the anterior (or upper) and posterior (or lower) endocardial cushions of the atrial canal (p. 19), but for a time there is an inter-atrial foramen, **foramen primum**, between the lower edge of the septum above and the endocardial cushions below. Before this foramen is closed, however, the upper part

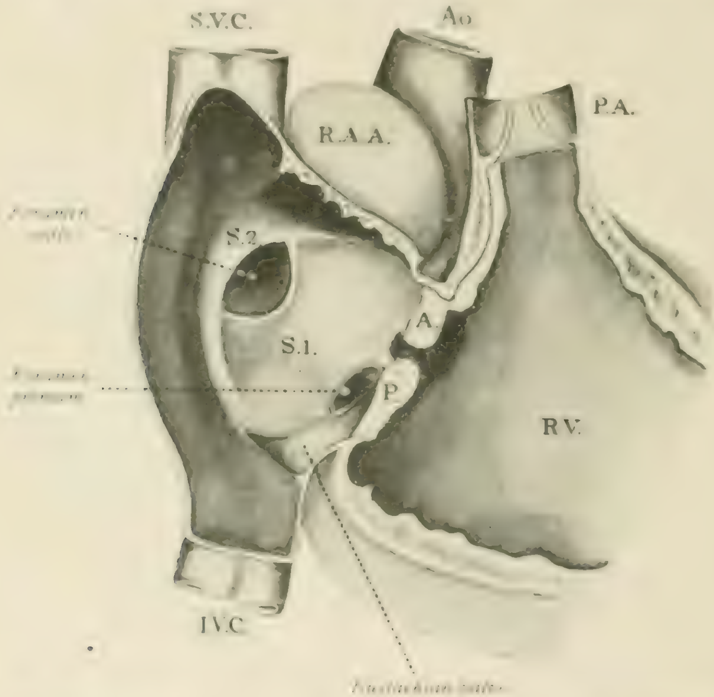


FIG. 28.—DIAGRAM OF THE RIGHT ATRIUM TO SHOW THE FORMATION OF THE ATRIAL SEPTUM. Ao., aorta; P.A., pulmonary artery; S.1, septum primum; S.2, septum secundum; A.P., anterior and posterior endocardial cushions.

of the septum is absorbed so that a new connection between the atria is formed; this is the **foramen ovale** (or foramen secundum). At first it is a wide opening, bounded below and in front by the now free upper edge of the septum primum; but later it becomes smaller and, by the growth of its ends, the free border of the septum primum faces upwards and forwards (fig. 29). (2) The **septum secundum** (BORN) is an infolding of the musculature of the roof of the atrium close to, and immediately on the right side of, the original attachment of the septum primum.[1] It closes the upper part of the foramen ovale. Its anterior and posterior extremities grow downwards on the front and back walls of the atrium towards the atrial canal, and its lower free concave edge at first faces downwards and forwards

[1] This infolding is described by His as a *muskulöse Leiste*, and it is said not to exist, in BORN's sense, in the pig by [illegible] (*Anat. Record*, vol. ii.); see also MORRILL, *Amer. Jour. Anat.*, vol. [illegible].

(fig. 28). The two septa, primum and secundum, by their continued growth soon overlap one another in front and behind; and by its unequal growth the free edge of the septum secundum changes its direction and faces downwards and backwards (fig. 29). The foramen ovale is now a slit-like passage between the free edges of the two septa; and the part of the septum primum which bounds it below, and which forms its left wall, is sometimes called the **valve of the foramen ovale**. The valve of the foramen ovale reaches the level of the lower edge of the septum secundum in the seventh or eighth month and at birth it overlaps it. The closure of the foramen ovale commences at birth when the left atrium becomes filled with pulmonary blood and the pressure in it becomes high enough to prevent blood entering it from the right atrium; the closure is assisted by an alteration in

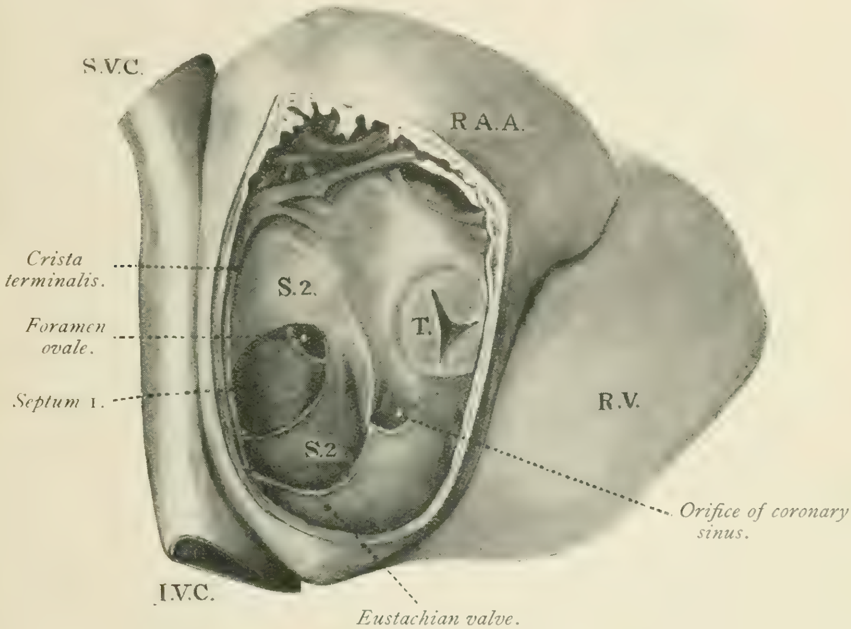


FIG. 29.—VIEW OF THE ATRIAL SEPTUM, AT A LATER STAGE, FROM THE RIGHT. (After TANDLER and BORN'S model of a 36 mm. embryo.)

T., tricuspid valve.

the action of the "limbic bands" (see below), brought about by their indirect attachment to the diaphragm which is now in use (KEITH). The foramen is not completely closed until the second year (HINZE), and, as was already stated, a slit-like remnant of it persists in about 25 per cent. of adult subjects; according to WALLMAN it more often persists in the female than in the male (see p. 34). It may be a double or multiple opening, and these conditions and the abnormal forms already described (p. 37) support ROKITANSKY'S contention that the normal closure is by a fenestrated membrane. (See also REID, *Jour. Anat.*, vol. xlvi.)

The two valves, the right and left **venous valves**, which guard the opening of the sinus into the atrium, fuse with one another above the opening and are continued into a ridge, **septum spurium** (HIS), which extends over the cranial wall, in front of the orifice of the superior vena cava, on to the anterior wall of the atrium; the two valves also fuse below the opening and are continued towards

the atrial canal where they fuse with the posterior endocardial cushion (fig. 13). In each valve a prominent band of muscle runs along the basal attachment of the free membranous part. Between the septum spurium and the left venous valve on the right side and the septum secundum on the left side, there is a part of the atrial cavity which is named the **spatium intersepto-valvulare**. It forms at first a well-marked dilatation on the cranial and posterior walls of the atrium (fig. 13), but at a later stage the left venous valve is applied to the surface of the septum secundum and the spatium intersepto-valvulare is obliterated. In the adult the remains of the valve may form a fretted membrane on the septal wall of the inferior vena cava and on the atrial septum behind the fossa ovalis (p. 32).

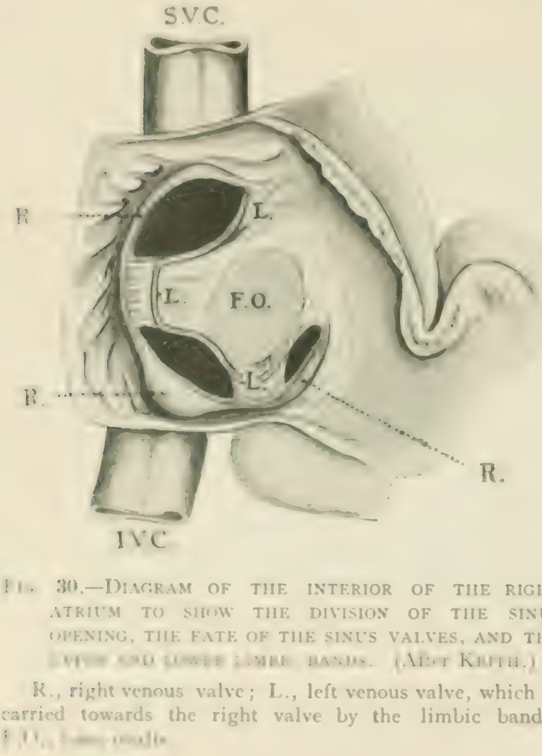


FIG. 30.—DIAGRAM OF THE INTERIOR OF THE RIGHT ATRIUM TO SHOW THE DIVISION OF THE SINUS OPENING, THE FATE OF THE SINUS VALVES, AND THE UPPER AND LOWER LIMBIC BANDS. (After KEITH.)

R., right venous valve; L., left venous valve, which is carried towards the right valve by the limbic bands; F.O., fossa ovalis.

The orifice of the transverse part of the sinus venosus becomes drawn into the posterior wall of the right atrium, and a septum, the sinus septum, develops between the openings of the inferior vena cava and the coronary sinus; and in this septum a band of atrial muscle, the lower limbic band (KEITH), appears and divides the lower part of the right venous valve into two parts, the Eustachian valve in front of the inferior cava and the Thebesian valve on the right side of the coronary orifice. A second inflection of the sinus wall is formed between the superior and inferior caval openings and in it the upper limbic band (KEITH) of atrial muscle forms (see further, p. 72). The original single sinus opening is thus divided into three parts. The upper part of the right sinus valve disappears, but the muscular band along its attached margin forms the prominent bundle of the **crista terminalis**; the **annulus ovalis**, on the other hand, represents the lower free edge of the septum secundum, which is reinforced by the upper and lower limbic bands, the musculature at the base of the left venous valve (fig. 30).

The **right atrium** is thus formed of three parts: (1) The right part of the primitive atrium, which forms all that part of the atrium, including the appendix, provided with musculi pectinati; (2) the right horn and right part of the transverse portion of the sinus venosus, which is the part of the atrium into which the venæ cavæ and coronary sinus open; and the original valvular opening of the sinus into the atrium is replaced, in part at least, by the sphincteric muscular bundles of the crista terminalis and the limbic bands; and (3) the right half of the atrial canal, which forms the smooth area above the atrio-ventricular orifice. (The morphological boundary between the atria and the ventricles is discussed on

p. 60.) The **left atrium** is also formed of three parts: (1) The left part of the primitive atrium, which forms the atrial appendix; (2) the left half of the atrial canal; and (3) the vestibular part of the atrium, which is formed by the inclusion in the atrium of the terminal parts of the pulmonary veins; it forms most of the atrium and is marked off from the remainder of the cavity by the tænia terminalis sinistra (KEITH, p. 72).

The early stages of the **development** of the **pulmonary veins** have been studied by SCHMIDT (in the pig), FLINT (*Amer. Jour. Anat.*, 1907), HIS (in the human subject), FEDOROW (*Anat. Hefte*, Bd. xl., 1910), BROWN (in the cat, *Anat. Record*, vol. vii., 1913), and others, and it seems to be well established that the pulmonary vein grows as a single (or double, VON MOLLENDORFF, *Anat. Hefte*, Bd. xlvii., 1913) vessel from the centre part of the sinus venosus, and, passing backwards in the venous dorsal mesocardium, reaches and anastomoses with a splanchnic plexus round the œsophagus and the pulmonary anlage; this plexus communicates freely with the neighbouring mediastinal plexus which drains into the systemic veins. As the sinus venosus shifts to the right and the sino-atrial orifice becomes defined, the pulmonary vein is found to open on the left side of the left venous valve and, when it forms, on the left side of the septum primum (on the left side of the septum superius and spina vestibuli of HIS); on the exterior of the heart the orifice is now on the left part of the area interposita. According to HIS the area interposita represents an extension of the sinus venosus into the left atrium, as is found in the amphibian heart; and, therefore, after the processes of inclusion of the pulmonary vein described below have taken place, the left atrium must be held to include a sinus area. It is not possible on histological grounds to distinguish a sinus extension beyond the left sinus valve, that is, the muscle first to develop there is atrial muscle; but as at the other sinus replacement areas it appears at a comparatively late period. The left atrium, though it may thus include a sinus extension, does not, however, include any of the sino-atrial junctional tissue as is found at the bases of the venous valves (see "Morphology of the Connecting Systems"); it would not appear, therefore, to have the morphological value of the right atrium. At its first appearance, in the Dipnoi, it is much smaller than the right atrium, and it is so even in the turtles among the reptiles; with the appearance of a complete ventricular septum, however, it must necessarily become as large as the right atrium. It has often been pointed out that in the dying heart (of amphibians and reptiles) the contractions of the left atrium cease before those of the right atrium (MILLS, *Jour. Anat.*, vol. xxii.), and HARVEY made the observation that in the mammalian heart the right atrium is the last chamber to die; it is commonly named *ultimum moriens*.

There is ultimately formed, as the venous return from the lungs, a single vein from each lung lobe, but in the root of the right lung the vessels from the upper and middle lobes join together, so that four stems proceed towards the heart. In the early embryo the veins form a common pulmonary trunk, as in reptiles; but as the lungs develop and pass round the heart the venous mesocardium is greatly widened and the left atrium increases in extent by the absorption into it of the stem of the common pulmonary vein, and later by the inclusion of the proximal parts of the two pulmonary trunks of each side. This included part of the pulmonary veins forms the vestibule of the atrium. The process of inclusion may be fully accomplished even though the sinus venosus remain distinct from the right atrium (see p. 126).

Development of the Atrial Myocardium.—The early stages of the atrial myocardium are comparable to those of the ventricular myocardium (see p. 58); but it is to be noted that

near the area where the posterior mesocardium (p. 15) is attached to it, the **area interposita** of His, the myo-epicardium is at first absent from the atrial wall. The differentiation of the atrial myocardium, however, occurs distinctly later than that of the ventricle; and with its occurrence muscle tissue invades the atrial septa and the venous valves. At a still later period the musculi pectinati appear, first in the appendages. The atrial musculature at this stage remains continuous with the ventricular musculature round the whole circumference of the atrial canal. The musculature of the coronary sinus and of that part of the atrium which is formed from the sinus venosus remains undifferentiated long after the remainder of the atrial muscle is defined, while the part of the left atrium which is formed from the pulmonary veins does not acquire cardiac muscle until a comparatively late period.

The Ventricles. A transverse section through the ventricles (fig. 12A, p. 64) shows that the ventricular septum is placed obliquely, running from before backwards and to the right; and further, that it bulges into the right ventricle, its right surface being convex and its left surface concave. The cavity of the left ventricle is thus circular in outline, while the right ventricle is crescentic, and the two are so placed that the right ventricle partly overlies the left ventricle in front. The walls of the lower parts of the ventricles are very irregular, being ridged with a large number of muscular columns, **columnæ carneæ**, of very varying size and of different form. Some of them are, as it were, only sculptured in relief on the ventricular wall, being attached to the wall in their whole length. Others, **trabeculæ**, are attached to the wall of the ventricle only by their extremities and are quite free, and often cross the cavity, between their attachments; this form is most abundant towards the apical parts of the ventricles, especially on the right side where they form a close network. A third set, **musculi papillares**, conical in shape, are attached at their bases to the ventricular wall and at their other ends are prolonged into fine tendinous cords, **chordæ tendineæ**, which are inserted into the cusps of the atrio-ventricular valves. The columnæ carneæ and the papillary muscles of the heart are advantageous arrangements of the cardiac musculature for the expulsion of the blood in systole, and especially at the beginning of that movement when the work of the heart is greatest; in the later phases of systole, it has been suggested, the chordæ tendineæ are relaxed. On the base of each ventricle (fig. 20) there are two orifices, a posterior **atrio-ventricular orifice** (ostium venosum, B.N.A.) and an anterior **arterial orifice** (ostium arteriosum, B.N.A.), which are, respectively, the entrance and the outlet orifices of the ventricular cavity. In its passage between these two orifices the blood may be said to traverse a V shaped course, corresponding to the two parts or limbs into which each ventricular cavity may be divided (fig. 20), namely, a posterior descending or "inflowing" limb and an anterior ascending or "outflowing" limb. The separation of the limbs is accomplished in part by one of the cusps of the atrio-ventricular valve and in part by other structures. Each of the orifices of the ventricles is guarded by a valve; these valves are named the **atrio-ventricular** and the **arterial valves**, and the two sets are quite different in their form. The right atrio-ventricular valve is usually named the **tricuspid valve** and the left one the **mitral valve**, while the arterial valves are named, respectively, the **pulmonary valve** and the **aortic valve**.

The name **valve**, according to HYRTL, was first used for the heart valves by BENEDICTUS; the Greeks named them [illegible], while VESALIUS named them *membranæ*. GALEN compared the arterial valves to the letter C in shape, while HEISTER introduced the name semilunar for them. The Greeks named the atrio-ventricular valves *triglochines* (γλωχιν, a point), and GALEN *tricuspides*, on account of their resemblance to a three-pointed spear head. VESALIUS suggested the name "mitral valve" for the left atrio-ventricular valve because of its resemblance to a bishop's mitre.

Atrio-ventricular Valves. The atrio-ventricular valvular systems consist of the following parts: (1) A number of firm membranous **cusps** or flaps, three on the right side and two on the left, which hang downwards into the ventricle from their attachment at the atrio-ventricular junction. (2) The **annulus fibrosus**, a ring of fibrous tissue at the atrio-ventricular junction, to which the bases of the cusps are attached. (3) The **chordæ tendineæ**, fine rigid tendinous cords, which are attached to the cusps from below. (4) The **musculi papillares**, from which the chordæ tendineæ arise.

In the fresh heart, and when healthy, the **cusps** are white, glistening, tendinous,

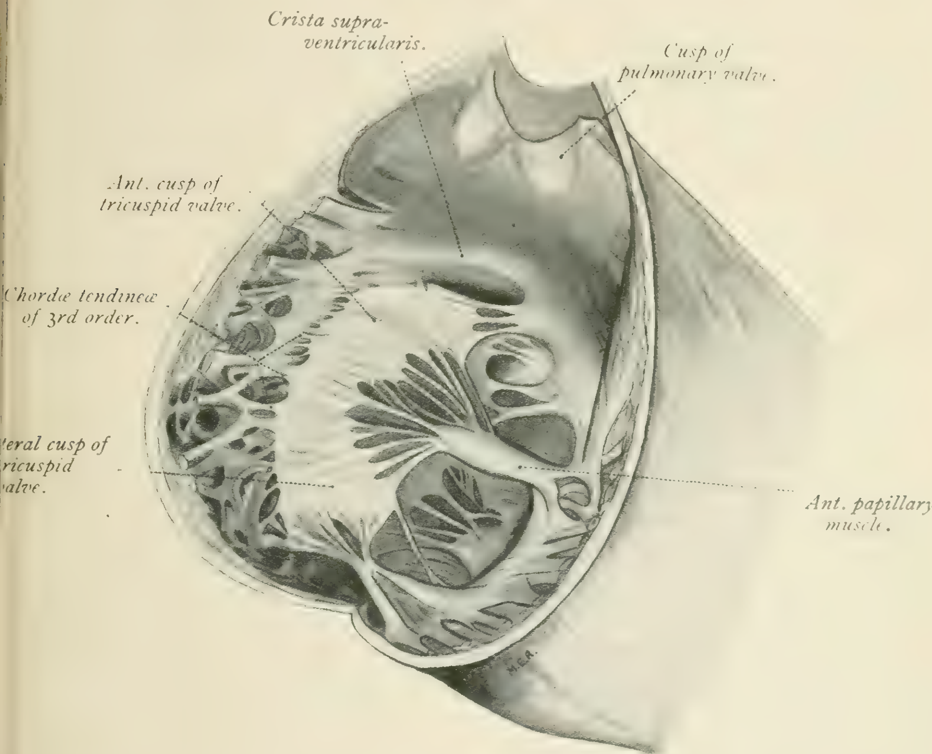


FIG. 31.—THE ROOF OF THE RIGHT VENTRICLE VIEWED FROM BELOW. (After TANDLER.)

curtain-like flaps, which are perfectly smooth on the atrial surface, but on the ventricular surface are ridged by the insertions of the chordæ tendineæ. They are united with one another at their basal attachments and for a varying distance along their adjacent margins, the separateness of the cusps showing great individual differences; and they form, therefore, a short slotted tube leading from the atrium into the ventricle. When looked at from the atrium the cusps appear to be continuations of the atrial wall and, as will afterwards be described, the atrial musculature is continued downwards in the atrial surface; but as viewed from below, they are separated from the ventricular wall by a perivalvular space. The walls of this space are ridged on the ventricular side by columnæ carneæ and on the valvular side by the chordæ tendineæ, and it is crossed, near the bases of the valves, by chordæ tendineæ of the third order (see below). In the right ventricle the perivalvular groove is reduced to a mere slit between the septal

cusp of the tricuspid valve and the septum, while in the left ventricle it is interrupted anteriorly and to the right by the origin of the aorta. The number of cusps is typically three on the right side and two on the left side, but smaller accessory cusps are very frequently found between the bases of the chief cusps. The free margin of the cusps is irregularly dentated, the apices of the dentitions being continued into the chordæ tendineæ. At these parts, and immediately above the margin, the cusps are considerably strengthened, but in the concave intervals between the dentitions the margin is much thinner. Close to the free border of the cusps on the atrial surface there are often to be seen, but more numerous and better developed at birth than in later life, small nodular thickenings of hyaline appearance, the **noduli Albini**. They were first described by CRUVEILHIER, but afterwards were more fully studied by ALBINI, who described them as consisting of a capsule formed by fibrous tissue, derived from the adjacent chordæ tendineæ, surrounding a core of more cellular tissue; and he compares them to the noduli Arantii. BERNAYS confirmed the descriptions of ALBINI and states that the nodules are remnants of the embryonic valve swellings. They are of importance on account of their similarity to pathological conditions, which indeed HENLE held them to be. There are also to be found very frequently on the cusps at birth (in 103 out of 120 hearts, PARROT) small red or dark red spots (hæmatomata) of millet-seed size on the ventricular surface close to the free margin. They are only very infrequently to be found on the semilunar valves. They were first described by ELSÄSSER, and all later writers are agreed that they are to be found chiefly in the newborn and that they disappear after the second year of life. The lining membrane of the hæmatomata is endothelial. There are two views of their origin, some (HAUSHALTER, MUNHARDT, WEGELIN) holding them to be cut off diverticula of the endocardium, while others (BERTI, KÖNIGER, HANNES, PARROT) describe them to be derivatives of the blood vessels of the cusps. About midway between the free border and the base of the cusps, a very distinct thickening of the cusp substance can be felt; this is produced by the insertions of the chordæ tendineæ of the second order (see below) which spread out in the cusp in an irregular network. The middle part of the aortic cusp of the mitral valve is free of this thickening, the passage of the chordæ tendineæ into it being different from the passage in the other cusps. Close to their bases isolated parts of the cusps appear more opaque than others, the atrial muscle being continued downwards at these places in pointed processes into the cusps.

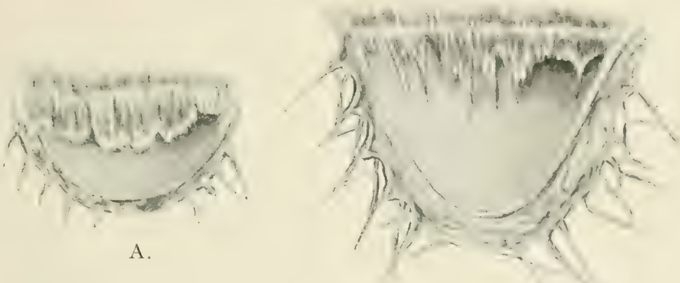
Histology of the Atrio-Ventricular Valves.—The structure of the atrio-ventricular cusps is a matter of considerable importance for they are a common site of disease processes; but it has been the subject of much controversy, the outstanding questions being the presence or absence of blood vessels in the normal cusps and the extension or non-extension of cardiac muscle into them.

Each cusp consists of a ground basis of fibrous tissue (lamina fibrosa) and a covering of endocardium which can be described as the atrial and ventricular layers continuous with one another at the free edge of the cusp. The lamina fibrosa, which differs greatly in thickness in the different cusps, probably directly on mechanical grounds, arises from and is perfectly continuous with the annulus fibrosus, but its substance is reinforced by the chordæ tendineæ which are attached to it. It consists of a poorly nucleated fibrous tissue, the fibres lying for the most part parallel to the long axis of the cusp, and contains only very few elastic elements; SEIPP states that the elastic elements are quite absent at birth. Of the two layers of endocardium on each cusp, the atrial layer is much the thicker; there are few differences, however, in the structure of the valvular endocardium from that of other parts of the heart (p. 27). The endothelial layer has the characteristic form. There is a thin sub-endothelial layer of hyaline appearance, and deep to this lies the lamina propria of the endocardium; in the atrial layer this is characterised by a large amount of elastic tissue, arranged in a network of fine and coarse fibres; the ventricular endocardium contains few elastic fibres. The sub-endocardial layer is a loose fibrous tissue, most apparent

on the atrial surface towards the bases of the cusps and gradually disappearing as it is traced towards the free edge.

Musculature of the Atrio-Ventricular Valves.—At early stages of their development (p. 58) the cusps of the atrio-ventricular valves are largely muscular, both the atrial and ventricular musculatures being continued into them. Subsequently the muscle undergoes retrogressive changes, but parts of it persist and, with their nutrient blood vessels, are to be found even in the adult. It is convenient to describe the atrial and the ventricular musculature separately.

Atrial Musculature.—The continuation of the atrial musculature into the atrio-ventricular cusps was described first by REID in the ox and the horse, and shortly afterwards by KRÜSCHNER and then more fully by SAVORY, JOSEPH, and GUSSENBAUER in man. GUSSENBAUER states that an atrial valvular musculature is of constant occurrence in man, the fibres being arranged longitudinally and reaching downwards to be inserted on the atrial surface at the level of the attachments of the chordæ tendineæ of the second order (see below) on the ventricular surface. The presence of atrial muscle in the cusps is now generally admitted, but while some (LANGER, DARIER, ODINZOW, TANDLER) describe it to be better developed and of greater extent in children, others (ALBRECHT and GUSSENBAUER) state that it is better developed in the adult. The aortic cusp of the mitral valve contains the greatest amount of muscle, but the order in which the other cusps should be arranged, as regards their muscle content, has been variously stated (GUSSENBAUER, ALBRECHT, LANGER). GUSSENBAUER gives the order as (1) aortic cusp, (2) anterior cusp of tricuspid, (3) septal cusp of tricuspid, (4) posterior cusp of mitral, and (5) posterior cusp of tricuspid; but



A. B.

FIG. 32.—THE ATRIAL MUSCULATURE OF THE AORTIC CUSP OF THE MITRAL VALVE.
A., in the newborn; B., in the adult.

there are probably individual differences as there certainly are great individual variations in the extent of the muscle, and by naked-eye examination it is sometimes impossible to detect any muscle at all. The endocardium must be very carefully removed; the muscle may tear off with it. Microscopic examination is much more satisfactory. The muscle consists of more or less isolated bundles which are continuous above with the atrial musculature and run downwards in the long axis of the cusp in the subendocardial layer. They do not extend beyond the upper third of the cusp, but end below in pointed processes on the atrial surface of the lamina fibrosa; ALBRECHT has stated that they become continuous with the chordæ tendineæ, but this is a matter of considerable doubt. The occurrence of transverse fibres in the cusps, as described by GUSSENBAUER, is somewhat doubtful, though the circular muscle of the atrium may at some places reach the bases of the cusps.

Ventricular Musculature.—The presence of rudiments of the extension of the ventricular musculature into the cusps of the atrio-ventricular valves was described first by BERNAYS, and subsequently in greater detail by ZÜCKERKANDL, LANGER, and HENLE. It occurs (in 20 per cent. of subjects in the anterior cusp of the tricuspid valve, ZÜCKERKANDL) in the form of a few isolated bundles which bend out of the ventricular wall and, passing either freely across the perivalvular groove or in its roof, reach the ventricular surface of the cusp at its base and run for a short distance towards the free border. They are most often to be found associated with the chordæ tendineæ of the third order (see below, and fig. 31) and may sometimes be followed to the insertions of the chordæ tendineæ of the second order. Muscle fibres extending from the papillary muscles to the cusps along the chordæ tendineæ are very rarely to be found, but isolated cases of their presence have been described.

The Blood Vessels of the Atrio-Ventricular Valves.—LUSCHKA, in 1852, described for the first time blood vessels in the valves of the heart; and though his descriptions of the

presence of blood vessels in the semilunar valves have not been established, the presence of vessels in the normal atrio-ventricular valves has been confirmed by a large number of writers (Gerlach, Foerster, Kölliker, Rosenstein, Sappey, Frey, Henle, Cohn, Gross, Spalteholz) and is now generally accepted. The chief opponents of the normal vascularity of the cusps have been the pathological anatomists, especially Rokitansky and Virchow, and they have been recently supported by Joseph and Camat. Langer, however, in a very complete work, which was subsequently confirmed by Darier and Odinzow, has demonstrated that, while the purely fibrous parts of the cusps are avascular, blood vessels are normally to be found with the muscular fibres. In early stages of development the vessels enter the cusps from above with the atrial musculature and from below along the muscular strands which become the chordæ tendineæ; but with the retrogression of the valvular musculature the vessels in large part disappear and are afterwards strictly confined in their distribution to the persisting muscle. (Even in the fœtus the chordæ tendineæ are avascular (Nussbaum) as they are transformed even then into tendinous bundles.) The cusps are more vascular at birth and in early life than later, and of the several cusps the aortic cusp of the mitral valve, as would follow from the descriptions given above of the valvular musculature, is the most vascular.

Nussbaum has recently described the arrangement of the valvular blood vessels in great detail, and has defined a vascular area of the cusps about 3 mm. broad running parallel with the base. In many mammals (pig, ox) blood vessels occur normally throughout the valve, but an extension beyond the musculature in man is probably always the result of inflammatory changes.

Chordæ Tendineæ.—The chordæ tendineæ are rigid glistening cords of fibrous tissue, covered with a thin closely adherent layer of endocardium. They are round or oval in transverse section. They spring, as a rule, in groups from the apices of the papillary muscles, but occasionally singly from small nipple-like muscular elevations, and in a few instances, and especially on the septum, directly from the ventricular wall. Each papillary muscle gives origin to a varying number (most commonly between four and ten) of main cords which in their course towards the cusps split into finer cords, and close to the cusp margin these may again divide into still finer cords; there is the greatest variability, however, in the mode of the subdivision. The manner of the insertion of the cords on the cusps has been made the basis of their arrangement in groups, and several schemes of grouping have from time to time been advanced (Senac, Kürschner, Sée, Henle, Tandler, and others). The grouping proposed by Tandler, and adopted here, with slight modification, is as follows (fig. 31):—

Group 1.—Chordæ tendineæ which are inserted on the free edge of the cusp. They are very numerous delicate threads which arise from the other cords near the cusp margin, and often form a fine network before they are attached to it.

Group 2.—Chordæ tendineæ which are inserted at intervals on the ventricular surface of the cusp from near its free edge, which they pass over, to the attached border. They are distinctly thicker than the chordæ of Group 1, and those attached to any one cusp are derived from two different papillary muscles or from one papillary muscle and the wall of the ventricle. At their insertions most of these chordæ spread out in a fibrous network which is attached to the lamina fibrosa and which produces the thickening of the cusp mentioned above as occurring about its middle part. Some of the cords, however, pass through the network to be inserted at the base of the cusp into the annulus fibrosus, an insertion which is also gained by a number of triangular tendinous processes which arise from the network itself. As a general rule, the stronger the cord the higher is its insertion on the cusp.

Group 3.—The chordæ tendineæ of this group, which were first described by Henle, can be seen only when the other chordæ are divided and the cusp is turned upwards. They will then be seen to be short broad fibres which stretch across the perivalvular groove from the ventricular wall to the under surface of the cusp near its base and to run along the cusp a short distance towards its free

margin. In certain animals they are fused to form a membrana chordarum (JARISH), and they are associated at some places with small slips of valvular ventricular muscle (p. 45).

False Tendons.—The name false tendons is given to fine tendinous cords which are often to be found in the ventricles in trabecular formation. Their presence has long been known and they were considered to be sufficiently described as aberrant chordæ tendineæ or atrophic trabeculæ; TAWARA, however, gave them a new significance by stating that they were anomalies in the distribution of the atrio-ventricular bundle tissue. This description has only in part been confirmed, for subsequent writers (ALSLEBEN, MÖNCKEBERG, DE WITT, RETZER) have found that some of these tendons contain no muscle fibres of any kind (true false tendons) or only ventricular muscle (trabecular tendons). The tendons which carry offsets of the atrio-ventricular bundle (three in ten, ALSLEBEN) may carry this tissue alone or in association with ventricular muscle. ENGEL states that false tendons are to be found in 50 per cent. of hearts, and describes as typical one which arises below the septum membranaceum and runs to the posterior papillary muscle of the left ventricle. In many animals larger parts of the atrio-ventricular system pass from the septum to the papillary muscles as false tendons. Their occurrence in the human heart is described by ACKERKNECHT (*Anat. Anz.*, Bd. lvi.).

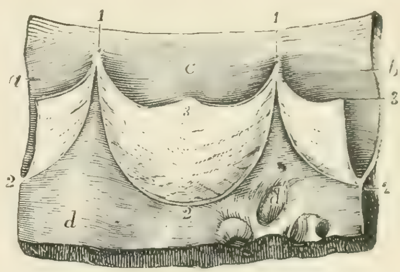


FIG. 33.—A PORTION OF THE PULMONARY ARTERY AND WALL OF THE RIGHT VENTRICLE WITH ONE ENTIRE SEGMENT AND TWO HALF SEGMENTS OF THE PULMONARY VALVE.

a, *b*, *c*, sinuses of Valsalva opposite the segments; *d*, *d′*, inner surface of the ventricle; 1, 2, curved attached border of the segments; 3, corpus Arantii, at the middle of the free border.

The Arterial Valves.—The arterial valves are placed at the roots of the pulmonary artery and the aorta, and are named the **pulmonary valve** and the **aortic valve**. Each valve consists of three approximately semilunar cusps, which are attached by their thickened convex margins to the arterial wall; while the free borders, slightly concave upwards, project into the interior of the vessel (fig. 33). The walls of the pulmonary artery and aorta are bulged out opposite each cusp, the bulged parts being known as the pulmonary and aortic **sinuses of Valsalva**; and with them the cusps form pocket-like cavities open upwards. The pointed triangular spaces between the cusps are known as the **spatia intervalvularia**. The position of the cusps varies, but most commonly, if they are examined while the heart is in its normal position in the body, there are two side cusps in front and one median cusp behind in the pulmonary artery, and one cusp in front and two side cusps behind in the aorta (fig. 23). The free edge of each cusp is raised a little at its middle and there is situated there a small nodular thickening, the **nodulus** or **corpus Arantii**. On each side of this there is a narrow semilunar area, adjoining the free edge, which is specially thin; these parts of the cusps are named the **lunulæ**.

The arterial valves close the arterial openings by the approximation of the free edges of the cusps when the pockets they form are filled; and the closeness of the contact is furthered by the thinness of the lunulæ and the presence of the noduli.

The **semilunar cusps** are transparent during youth, but later in life they

become perfectly opaque. The aortic cusps are thicker and more tendinous in appearance than the pulmonary cusps, but the noduli of the pulmonary cusps (sometimes called the noduli of Morgagni) are larger and more prominent than the noduli of the aortic cusps. The lunulæ, and occasionally larger parts of the cusps, are sometimes fenestrated, without any apparent disturbance of the valve mechanism; fenestration is more common in the male than in the female and in the aortic than in the pulmonary cusps (SIMPSON, *Jour. Anat.*, vol. xxxiii.). Small nodular excrescences, first described by LUSCHKA and LAMBL, are sometimes to be found on the inner surface of the aortic cusps. On close naked eye examination of the cusps, especially when stretched, delicate curved thickenings, lying concentric with the free border, can be seen; they extend from the attached border to the noduli. The noduli fill the central space that would otherwise remain when the valves close and, as suggested by EWALD, they may act as interlocking teeth which hinder the slipping of the cusps on one another. Irregularities in the number and arrangement of the cusps are occasionally seen. The most common irregularity is the presence of a fourth cusp in the pulmonary valve; when four cusps are present they may or may not be of equal size. (See further, DELITZIN, *Arch. f. Anat. u. Phys.*, 1892.) An additional cusp in the aortic valve is of rare occurrence. Either valve may consist of two cusps, and the pulmonary valve has been seen formed by a single cusp; other anomalies of the pulmonary valve, for example when the cusps are fused together forming a diaphragm with a small central aperture, often accompany defects in development of the heart. The description of the **position of the cusps** given above is that usually followed by English anatomists, but Continental writers (and the B.N.A.) describe one pulmonary cusp in front and two behind, and two aortic cusps in front and one behind. The English description is usually attributed to GIBSON, though the work in which it is first stated is unknown, while the Continental description was first given by VESALIUS. In an examination of 100 bodies, WINDLE (*Proc. Anat. Soc., Jour. Anat.*, vol. xxix.) found the arrangement described by VESALIUS in 15 subjects, and the arrangement described by GIBSON in 85 subjects. The difference is, of course, entirely topographical, for the developmental relations of the two sets of valves are maintained; what is named here the right cusp of the aortic valve is really the posterior cusp of development, as is maintained in the B.N.A., and the left cusp of the pulmonary valve is the anterior cusp (fig. 23). A criticism of the English nomenclature is given by MALL (*Amer. Jour. Anat.*, vol. ii.). A convenient nomenclature for the aortic cusps is right and left coronary cusps for those opposite the origin of the right and left coronary arteries and non-coronary cusp for that opposite the vacant sinus.

The **sinuses of Valsalva** are bounded distally by a ridge, often irregular in its course, which lies a little distance above the level of the free edge of the cusp. In the young, and even more so in the newborn, the upper parts of the sinuses are separated by short vertical ridges which ascend on the vessel wall from the place of common attachment of two cusps (fig. 33); in later life these ridges disappear. They are hyaline in appearance and correspond to **thickenings of the vessel walls.**

Histology of the Semilunar Cusps. The semilunar cusps consist of three layers, namely, a middle fibrous tissue layer and two covering layers, which are formed on the one side by a prolongation of the ventricular endocardium and on the other by a continuation of the lining coat of the artery. The ventricular layer is smooth, but the arterial layer shows fine transverse folds. [illegible] described the ventricular and arterial layers to be similar in their structure, but more recently MÖNCKEBERG (in the aortic valve) and TORRIGIANI (in the pulmonary valve) have shown that they are in fact quite different. In the following account MÖNCKEBERG'S descriptions have been adopted: **(1) The middle fibrous tissue layer, which is much thicker in**

the aortic than in the pulmonary cusps, consists of transverse and longitudinal fibres. The nodular thickenings at the attachments of the cusps, especially of the aortic cusps, which are common in old age, are due to the deposition of fat in this layer. (2) The ventricular layer of endocardium consists of three strata: (*a*) a subendothelial fibrous-tissue zone with numerous fine elastic fibres mostly longitudinal in direction; (*b*) a layer which remains yellow after Van Gieson's stain, rich in nuclei and with numerous fine elastic fibres arranged transversely; (*c*) a fibrous-tissue zone in which there are few elastic fibres. At the boundary between (*b*) and (*c*) there is an elastic lamina similar to the lamina elastica interna of an artery wall. (3) The arterial layer is, as a rule, the thickest layer of the cusp. It consists of (*a*) a narrow subendothelial zone and (*b*) a broad zone of compact fibrous tissue arranged transversely, in which there are only a few fine elastic fibres.

In the lunulæ the middle fibrous layer is absent, while at the noduli it is much thickened and also looser in texture. At the insertions of the cusps, zones (*a*) and (*b*) of the ventricular layer are continued into the subendocardial layer of the ventricle, while the fibrous-tissue zone (*c*) is continued into the annulus fibrosus of the arterial root; the fibrous tissue of the arterial layer is continued into the fibrous tissue of the media of the artery wall and the subendothelial zone passes into the intima.

It is now generally agreed that normally there are no blood vessels in the semilunar valves. LUSCHKA, however, held that vessels were normally present in them, and he was supported in this view by KRAUSE and ROSENSTEIN; all subsequent writers, however (KÖLLIKER, JOSEPH, LANGER, HENLE, FREY, SAPPEY, COEN, NUSSBAUM, DARIER, GROSS, and others), have been unable to discover any evidence of normal vascularity; and further, ODINZOW has examined the cusps in the fœtus and states that in the six months old fœtus no vessels are to be found. In pathological changes in the valves, it has always been admitted, vessels may be seen throughout the entire extent of the cusps. Recently, however, BAYNE-JONES has described a successful injection of normal aortic and pulmonary cusps and thus reopened the whole question of the vascularity of the arterial heart valves and, therefore, of embolic endocarditis.

Structure of the Arterial Root.—The structure of the wall of the sinuses of Valsalva cannot be understood without reference to the structure of the arterial root as a whole; and of this matter only a general description will be given here on account of the developmental complexities which are involved. It may be simply stated that at each of the arterial openings there is a short tubular zone formed of fibrous tissue, the proximal and distal borders of which, at its junctions with the ventricular muscle and with the typical arterial wall respectively, are uneven (fig. 45). This zone is a derivative of the bulbus cordis segment of the heart, as are also the semilunar valves which are found on its inner surface. Since the valves are derived from the proximal ends of the distal bulbar swellings (p. 62), it follows that the part of the fibrous zone which lies between the attachments of the valves and the lower end of the typical arterial wall is derived from the distal part of the bulbus; and the irregularity of its distal margin is due to the uneven advance of the arterial wall into the bulbus wall. The part of the fibrous zone which lies proximal to the valves is the rudiment of the ventricular part of the bulbus, the muscle tissue of which has disappeared; the proximal part of it is included in the heart and covered with ventricular muscle, but the boundary between the two parts is irregular on account of the irregular distal excursion of the ventricular muscle.

The boundary between the ventricles and the arteries, in the functional sense, is easily defined as the line of attachment of the semilunar valves. It will be apparent, however, from what has been said above, that the morphological boundary by no means corresponds to the functional boundary; that the ventricle cannot be considered to extend upwards as the spatia intervalvularia nor the artery to extend downwards as the sinuses of Valsalva. HENLE was the first to draw attention to this difficulty of defining the ventriculo-arterial boundary and introduced the term "arterial root" (the fibrous zone mentioned above) to replace the term "arterial ring" by which this boundary had been previously defined; and he described the unevenness of the margin of the ventricular muscle—in a general way that it reaches highest in the spatia intervalvularia and that at certain places it reaches above the valve attachment. LUSCHKA, however, was the first to describe the fibrous zones and their connections in detail. According to him, and to TORRIGIANI, there is, at the root of each artery, a circular, almost cartilage-like zone in the form of three arches concave upwards, the arches being flatter than the arches formed by the valve attachments, but their ends coincident with the apices of the spatia intervalvularia. On the right side (annulus arteriosus dexter) the convexity of the arches rests directly on the ventricular-muscle substance; on the left side, however (annulus arteriosus sinister), the fibrous substance of the left arch is continued downwards into the aortic cusp of the mitral valve and that of the right arch into the pars membranacea septi. (See further, "Skeleton of the Heart.")

The wall of the sinuses of Valsalva, then, consists in part of arterial wall and, at a varying distance below this, of the fibrous tissue of the "arterial root," in which there is little or no elastic tissue, and which is continuous with the fibrous tissue of the cusps of the valves at their

[illegible] with the fibrous tissue of the ventricular musculature. At the transition of the artery into the "arterial root" the elastic tissue of the arterial wall becomes gradually less and ends in a pointed projection which lies close to the internal coat. The wall, as it were, is bevelled off, the outer parts of the media ending at a higher level than the inner parts; and this bevelled part is embraced on the exterior by the conversely bevelled upper part of the fibrous "arterial root." The thickness of the vessel is thus reduced in the sinus, on an average, to about one-half. The intima of the artery is also thinned as it passes into the sinus.

The level of the line of transition from the artery to the arterial root is the same in all three sinuses of the pulmonary artery, the distance between the valve attachments and the arterial wall being greatest at the middle of the sinuses, where it is about one-third of the length above the cusp margin, and least at the sides. In the aorta the level is different in the three sinuses; in the right sinus the elastic tissue of the arterial wall reaches nearly to the line of the cusp attachment, in the left sinus about three-quarters of the way down, and in the anterior sinus the vessel wall ends at approximately the same level as in the pulmonary artery. The upward extension of the ventricular musculature is greatest in the left sinus of the pulmonary artery, the greater part of the cusp of this sinus being attached to muscle tissue; in the posterior pulmonary sinus the musculature reaches just to the attached border of the cusp, while in the right sinus it reaches a little beyond it. LANGER has stated that in the child the attachment of the cusps is higher and is not surrounded by ventricular muscle. As already stated, the fibrous tissue of the aortic root is continued downwards, on the left into the anterior cusp of the mitral valve, and on the right into the septum membranaceum.

Right Ventricle The cavity of the right ventricle, as is well shown on a cast of it, has the form of an irregular three-sided pyramid, the apex of which is at the origin of the pulmonary artery, while the walls are as follows: (1) A medial or septal convex wall, which bulges into the cavity so that in cross section the cavity is crescentic in form (fig. 12); (2) an antero-lateral bulged out wall, which corresponds to the sterno-costal surface; (3) a postero-inferior flat wall, which corresponds to the diaphragmatic surface and forms the base of the pyramid: it passes, without definite boundary, into the antero-lateral wall at the margo acutus, but, like it, it is separated from the septal wall by a definite groove; and (4) a narrow upper wall or roof, which runs forwards and to the left from the atrio-ventricular to the arterial orifice (fig. 34).

Between the venous and arterial orifices the roof of the right ventricle projects downwards in the form of a thick rounded muscular ridge, 12 to 15 mm. high, the **crista supraventricularis** (figs. 31 and 34). This ridge divides the upper part of the ventricular cavity into a posterior "inflowing" or atrial part, into which the atrio-ventricular orifice leads, and an anterior "outflowing" part which leads upwards into the pulmonary artery; this latter part, already recognised on the exterior of the heart, is named the **conus arteriosus** or **infundibulum**

The **crista supraventricularis** (B.N.A.) was first accurately described by WOLFF (1871) and though not definitely named by him, is usually called *éperon de Wolff* by French writers; PETTIGREW named it the fleshy pons, and SAPPEY, CRUVEILHIER, and SÉE the *muscle compresseur de la valvule tricuspidale*, SÉE comparing it with the powerful muscular compressor of the tricuspid orifice of birds (p. 11). HENLE describes it as a muscular bridge which corresponds with and forms a substratum for the beginning of the aorta from the left ventricle; but it is to be noted that the ridge is not produced by the aorta but by a definite muscle bundle which begins on the antero-lateral wall and arches medially across the roof between the two orifices of the ventricle, and is a derivative of, or at least is in the position of, the bulbo-auricular fold (p. 19) of the embryonic heart. The term conus arteriosus was applied to the arterial part of the ventricle by WOLFF, and infundibulum was first used by SAPPEY, CRUVEILHIER, and POIRIER; SÉE names it the pulmonary funnel. A space of varying depth lies between the crista supraventricularis and the anterior (or infundibular) cusp of the tricuspid valve.

The convex antero-lateral wall, which is relatively thin, is richly set with columnae carneae, the larger masses of which lie parallel with the long axis of the cavity. Posteriorly they reach upwards to the basal attachments of the

tricuspid valve flaps, but anteriorly, when followed upwards, they become gradually smaller and ultimately disappear, so that the interior of the conus arteriosus is smooth.

The posterior wall is covered with columnæ carneæ in its whole extent (fig. 35).

The convex medial (or septal) wall can be divided into two parts, an upper

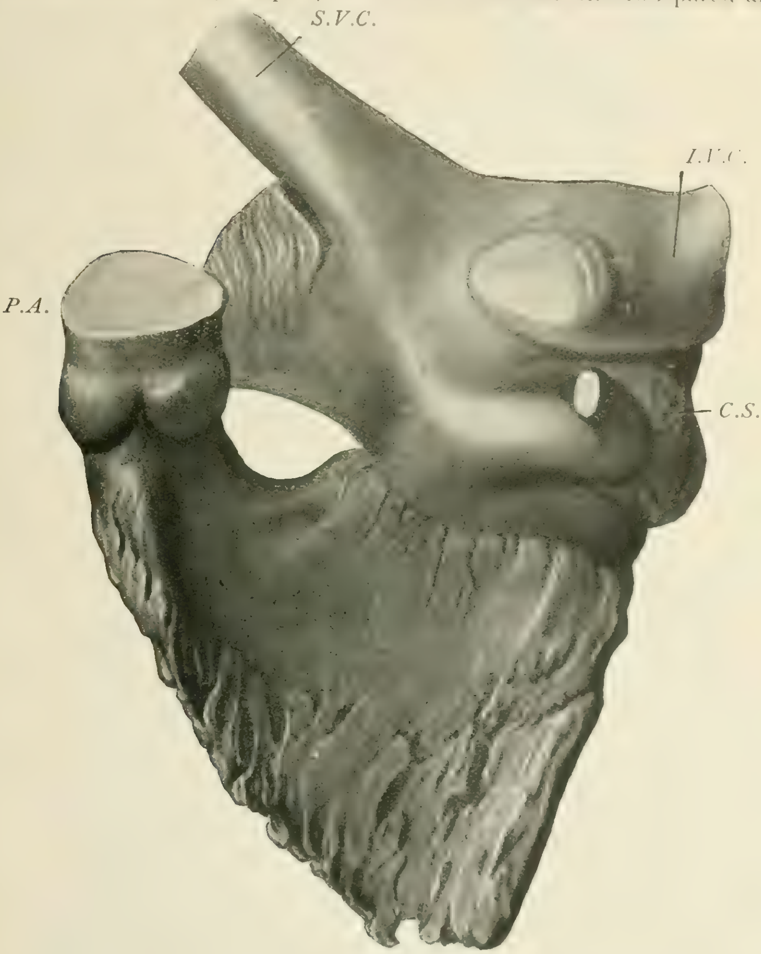


FIG. 34.—CAST OF THE INTERIOR OF THE RIGHT ATRIUM AND VENTRICLE. ($\frac{5}{9}$ nat. size. From Tandler's "Anatomie des Herzens" (GUSTAV FISCHER, Jena).)

The cast is viewed from the septal side. The impression of the fossa ovalis is seen on the atrial part. The separation of the ingoing and outgoing parts of the ventricle is shown. *S.V.C.*, superior vena cava; *I.V.C.*, inferior vena cava; *P.A.*, pulmonary artery; *C.S.*, coronary sinus.

smooth part and a lower richly trabeculated part; on the larger upper area, it is true, there may be seen the origin of numerous chordæ tendineæ and also large flattened ridge-like muscle bands, but these are not raised from the wall as typical trabecular formations. At the upper part of this area, immediately below the septal end of the crista supraventricularis, lies the **pars membranacea** of the ventricular septum, covered by the medial (or septal) cusp of the tricuspid valve. At the junction of the upper and lower parts of the septal wall there arises a trabecular formation, very variable in its amount and in its form, which

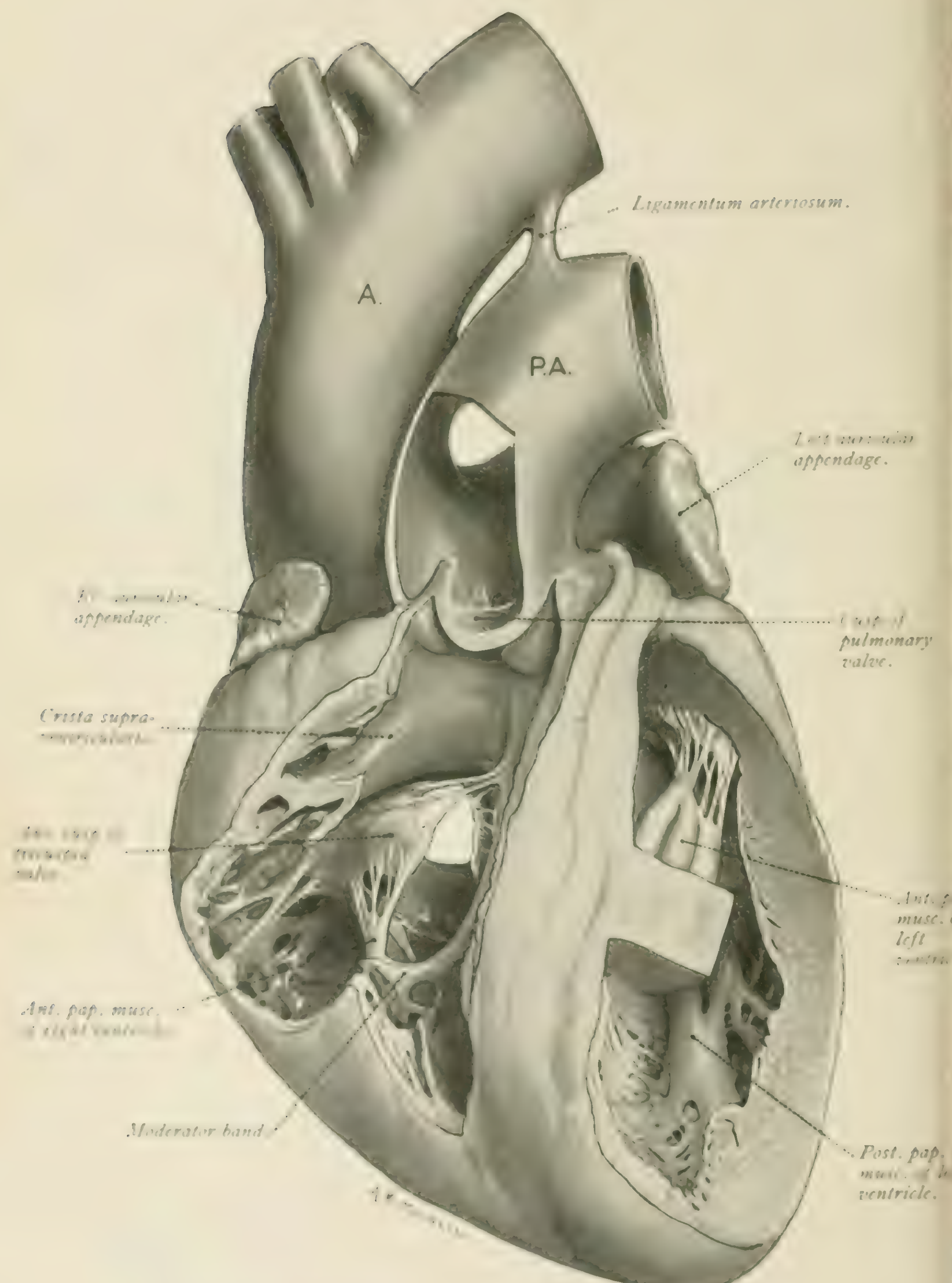


FIG. 35.—A DISSECTION OF THE VENTRICLES, VIEWED FROM IN FRONT. (A. K. MAXWELL.)

stretches across the lower part of the ventricular cavity and ends on the antero-lateral wall (fig. 35). The uppermost part of this formation is usually a more or less isolated rounded trabecula; it is named the **moderator band** (trabecula septo-marginalis, TANDLER; trabecula supraventricularis, RETZER).

The upper smooth part of the **septal wall** can readily be divided into two parts, one, which forms the medial wall of the conus, in front of the crista supraventricularis, and the other, which forms the medial wall of the "inflowing" part of the ventricle, behind it. The name **moderator band** was first used by KING (1837). He studied it in different mammals and named it the moderator band of distension, for he believed it prevented a too great distension of the right ventricle in diastole. According to HOLL, LEONARDO DA VINCI figures it very accurately in one of his drawings, and, as TANDLER points out, it appears to be indicated in a drawing by VESALIUS. POIRIER names it the *bandelette ansiforme*, and TESTUT the *faisceau arqué*. There can now be no doubt, though it has been described as a variation by several authors, that this band is a typical and proper formation of the right ventricle and that, as the crista supraventricularis and the anterior cusp of the tricuspid valve separate the two parts of the ventricular cavity above, it separates the two parts below. It has been very fully studied by RETZER (whose nomenclature, however, has not been adopted here), who has demonstrated that in many species it consists only of fibres of the atrio-ventricular conducting system (bundle of His), and as is indicated in the section on comparative anatomy (p. 9), TANDLER has described it to be the homologue of the right part of the septum of the general reptilian heart and named it the trabecula septa-marginalis. As has already been stated, the moderator band shows many variations in its form and size; it may be a stout muscular bundle or a thin thread-like cord. In some instances it is considerably broadened at its origin and reaches upwards on the septum to the crista supraventricularis; in others it springs from the septum as a narrow sharply circumscribed band. Its course from the medial to the lateral wall shows few variations, but the number and arrangement of the trabeculæ which run from its under surface to the apical region of the heart are very variable. At its termination on the antero-lateral wall it is always connected by trabeculæ to the anterior papillary muscle (see below).

The two parts of the cavity of the right ventricle are readily distinguished, especially in the systolic heart when the opening between them, bounded above by the crista supraventricularis, below by the moderator band, and at the sides by the extension of these parts on the septum and the anterior wall, is often a small circular foramen; and it may be noted here that in the early stages of dilatation of the right ventricle it is the posterior "inflowing" chamber alone which is affected.

The **tricuspid valve** guarding the right atrio-ventricular opening, is composed of three cusps; yet, though this description has been applied to it from ancient times, almost always smaller or larger accessory cusps are to be found at one or all of the angles between the principal cusps. Of the three cusps (fig. 46) one, which is usually the largest, is situated at the anterior and left part of the opening and projects downwards between it and the infundibulum (conus arteriosus) (fig. 35); it is, therefore, usually named the **infundibular** (or anterior) **cusp**. It is irregularly quadrilateral and is attached above to the anterior part of the annulus fibrosus (fig. 46). The second cusp, named the **right** (or posterior) **cusp**, lies at the right and posterior part of the opening, its attachment to the annulus fibrosus extending from near the margo acutus to the septal wall. The third, the **septal** (or medial) **cusp**, lies close to the ventricular septum; it is the smallest cusp. It is attached above not only to the annulus fibrosus but also to the ventricular septum, its most anterior part reaching the pars membranacea. The atrio-ventricular orifice is almost circular in the distended heart, but is more oval in the empty heart; its circumference measures, on an average, 122 mm. in the male and 115 mm. in the female (see p. 122).

The names applied to the three cusps of the tricuspid valve have varied very much at different times and vary even still among different authors; but the only other terms which require to be noted here are marginal and inferior (POIRIER) which have been applied to the right or posterior cusp, the latter name being specially applicable if the heart be considered to lie in its normal position in the chest. The most common variation of the cusps is the division of the right

cusp or the presence of an accessory cusp between it and the septal cusp, the tricuspid valve very frequently possessing four cusps (MORISON). On the other hand, the division between the right and infundibular cusps is often indistinct. Variations of the tricuspid segments are not confined to the human subject, being equally frequent among most mammalia (BEDDARD, WEIDERSHEIM). The attachment of the septal cusp is frequently as much as ·5 cm. below the plane of the atrio-ventricular orifice.

The **papillary muscles** of the right ventricle show many variations. The most constant and the largest is the **anterior** papillary muscle which springs as a single mass from the antero-lateral wall about midway on its length. It arises, nearly always, also from the moderator band and the trabeculæ associated with it, and in some instances this origin is largely developed and the direct attachment to the ventricular wall is small or even completely absent. At its summit it gives origin, sometimes directly, sometimes after division into secondary muscle columns, to ten or twelve chordæ tendineæ which lie in the cleft between the infundibular and posterior cusps and are attached to both, but in the main to the former cusp. The **posterior** papillary muscle is more irregular in size and position and is often represented by two or three smaller masses, arising, most commonly, in the angle between the posterior and septal walls; and the chordæ tendineæ proceeding therefrom are attached to the posterior cusp and the posterior part of the septal cusp. A third set of small **accessory** muscles and short chordæ tendineæ which arise directly from the ventricular wall is constantly to be found in the right ventricle; they are attached chiefly to the septal wall and are inserted into different parts of the cusps. One of the muscles (medial papillary muscle, LANCISIUS; the papillary muscle of the conus, LUSCHKA) is easily recognised in the majority of hearts; usually 6 to 8 mm. long, it is attached on the medial wall of the conus close to the lower end of the crista supraventricularis and its chordæ tendineæ are inserted into the adjacent borders of the septal and infundibular cusps. If the muscle be absent the chordæ tendineæ spring from a small superficial tendinous area (macula tendinea septi, HOLL). The infundibular and posterior cusps have relatively large numbers of chordæ tendineæ of the third order (p. 46) attached to them (fig. 31).

The **pulmonary orifice** is situated immediately in front of the orifice of the aorta and in front of and a little medial to (that is to the left of) the tricuspid orifice and also at a slightly higher level (fig. 46). It is circular in outline and, on an average, measures 72 mm. in circumference in the male and 68 mm. in the female (see p. 125). The three cusps of the valve which guard the opening are arranged two in front, right and left anterior, and one behind (p. 48).

Left Ventricle.—The left ventricle is of a conical form, the smaller end forming the apex of the heart, while on the base there are the venous (atrio-ventricular) and arterial (aortic) openings. It is longer and narrower than the right ventricle. It can, like the right ventricle, be divided into "inflowing" and "outflowing" parts, though the separation is effected in a different manner. A more significant division is that into supra-papillary and inter-papillary parts, the free ends of the papillary muscles marking the boundary between the two (HESSE and ALBRECHT). In systole of the heart the inter-papillary cavity is obliterated but the supra-papillary space remains patent even in the strongest contractions (p. 65).

The left ventricle has **lateral** and **medial** walls, both of them concave towards the cavity. They are two or three times thicker than the walls of the right ventricle, and since the curvature of the heart is there sharpest they are thinnest at the apex of the heart. The lateral wall is sometimes divided into ventral and dorsal parts, but there is no distinct boundary between the two, the whole wall corre-

sponding to the sterno-costal, left (margo obtusus), and diaphragmatic surfaces of the exterior. It is beset in the whole of its extent with a thick network of trabeculæ. These are smaller than in the right ventricle, but are more numerous and more closely reticulated, and at the apex of the heart the reticulation is so great in amount that this region appears like a cavernous tissue; towards the base of the heart the trabeculæ become larger. Bands similar in appearance to the moderator band of the right ventricle are not uncommonly found crossing the lower part of the cavity, sometimes between the bases of the papillary muscles and sometimes from the septum to the anterior papillary muscle; the latter contain fibres of the atrio-ventricular bundle. The medial wall is formed by the **ventricular septum**; it is triangular in shape, the apex being at the apex of the heart, while the base is fused with the atrial septum. It is beset with trabeculæ only in its lower third, the upper two-thirds being perfectly smooth. The fore part of the smooth area is limited above by an arched ridge, concave upwards, which runs from behind forwards to the arterial orifice; it is named the limbus marginalis (HIS). Immediately above it and forming the highest part of the septal wall there is a small area in which muscle fibres are absent and the septum consists only of a little fibrous tissue between two layers of endocardium; this area is known as the **pars membranacea septi**.

In general the **trabecular network** of the left ventricle has rounded meshes, in contrast with the elongated meshes of the right ventricle. Close to the apex of the heart there are often to be seen trabeculæ which consist, not of muscle substance, but entirely of tendinous fibres, the so-called trabeculæ tendineæ (see "False Tendons," p. 47). On the dorsal part of the lateral wall the trabeculæ reach to the attached margins of the mitral cusps, but on the ventral part they end nearly an inch (1·5 to 2 cms.) below the base of the heart. In the fresh heart there can be seen on the upper smooth part of the medial wall a network of fine fibres which lie just below the endocardium; in part, at least, this formation belongs to the left limb of the atrio-ventricular bundle (p. 83).

The **pars membranacea septi** appears to have been noted first in 1831 by SCHLIEMANN, who described it, however, as a pathological formation. In 1838 THURNAM recognised that it was a normal part of the septal wall and described it as follows: "The highest part of the septum, which occupies the angle between the posterior and right aortic valves" (the right and anterior valves of this work), "is in the human subject formed not of muscular fibres, but simply of the endocardium of the right and left ventricles and strengthened only by the interposition of a little fibrous tissue continuous with that of the aorta." The name pars membranacea was given to it by REINHARD in 1857. Its thickness is as a rule about 1 mm., but it may be thinner; it is, therefore, transparent and is easily recognised immediately below the aortic orifice if the septum be held to the light. It varies considerably, however, in its size and form. If it be examined from the left side (fig. 37) it is seen to lie immediately below the adjacent parts of the anterior and right cusps of the aortic valve, and to extend backwards beyond the middle line of the right cusp almost to the posterior end of the attachment of the mitral valve. Its lower convex border, along which the septal musculature abruptly ceases, is the most distinct, and the ventral boundary is only a little less definite; the upper and dorsal part, however, is continued upwards into the tissue of the "aortic root" in the right spatium intervalvularia (p. 49) and is, therefore, not defined. If this upward process be large the septum membranaceum has a triangular shape, but if it be small the septum is of an oval form. To examine the septum from the right side (fig. 36) the septal cusp of the tricuspid valve must be removed so that only its attached margin remains. It will then be seen that the line of attachment of this cusp crosses the septum and divides it into two parts. The lower of these, situated at the posterior end of the crista supraventricularis, intervenes between the two ventricles; it is formed behind the lower end of the bulbar septum at the fusion of the ventricular septum with the anterior endocardial cushion (fig. 28). The upper part separates the right atrium from the left ventricle, as was first noted by LUSCHKA and HENLE; it has been named the septum atrio-ventriculare (HOCHSETTER). In the right atrium it lies in front of the limbus fossæ ovalis and just above the base of the septal cusp, and in the fresh heart it is usually bulged a little and is lighter in colour than the surrounding parts, the atrial musculature being absent from its surface. If a needle be passed through it here it passes into the left ventricle between the right and anterior aortic

cusps. This portion is derived from that part of the fused endocardial cushions which lay between the attachments of the atrial and ventricular septa (fig. 40 and p. 60).

The pars membranacea consists of fibrous tissue (with elastic fibres, SEIPP) covered on both sides with endocardium. Isolated muscle fibres are said to be found in it not infrequently (W. GRUBER), but their presence has not been generally recognised. Interventricular foramina in the position of the septum are common congenital lesions (p. 128). In the ox, as in most

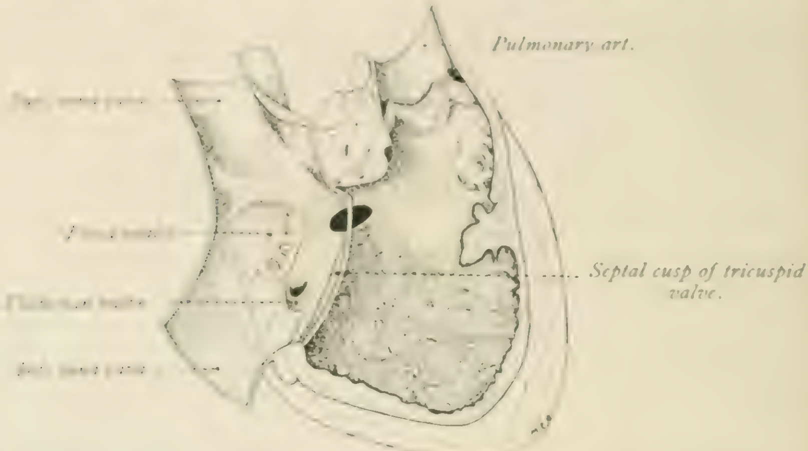


FIG. 36.—DIAGRAM TO SHOW THE POSITION AND RELATIONS OF THE PARS MEMBRANACEA SEPTI (IN SOLID BLACK) FROM THE RIGHT SIDE.

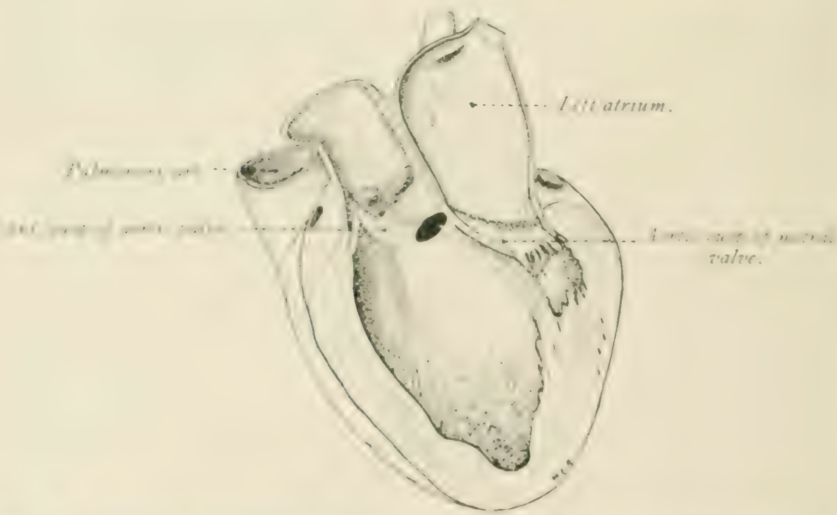


FIG. 37.—DIAGRAM TO SHOW THE POSITION AND RELATIONS OF THE PARS MEMBRANACEA SEPTI (IN SOLID BLACK) FROM THE LEFT SIDE.

mammals, the membranous septum is covered on the left side by the musculature of the ventricular septum which reaches up to the aortic root (musculus subaorticus, JARISH); remnants of this subaortic muscle are occasionally to be seen in man.

The mitral orifice, on an average, is 103 mm. in circumference in the male and 100 mm. in the female (see p. 122). It is guarded by the **mitral valve**. The valve is formed by two cusps, named the **anterior** and **posterior cusps**

(right and left cusps by French writers); but on account of its relations to the aortic opening the anterior cusp is often named the **aortic cusp** (fig. 46). The anterior cusp, a triangular plate 15 to 18 mm. long at its middle part, is longer and narrower than the posterior cusp; it projects into the ventricle between the atrio-ventricular and aortic orifices. It is attached above to the anterior and medial parts of the annulus fibrosus, but from the surface it is difficult to define the position of its base; for its atrial surface lies on the same plane as the atrial wall and, moreover, the atrial musculature is continued into its substance (p. 45), while the ventricular surface is limited only by the attachments of the aortic valves, the fibrous tissue of the cusp being continuous with that of the aortic root. The posterior cusp, square shaped and 10 to 12 mm. broad, springs from the posterior and lateral parts of the annulus fibrosus; its base can be more easily defined than that of the anterior cusp. The two cusps are separated by clefts which reach to the annulus. Accessory cusps are not commonly found, though the posterior cusp has been seen divided into two parts (TURNER, *Jour. Anat.*, vol. xxxii.).

The **papillary muscles** of the left ventricle are typically two in number; and are larger than those of the right ventricle. They lie opposite the intervals between the mitral cusps and are attached by their bases directly to the ventricular wall at about the junction of the apical and middle thirds; they seldom have any extensive trabecular connections. The **lateral** muscle springs from the concavity of the antero-lateral wall and the **medial** muscle from the angle between the posterior wall and the septum. There are great variations in the form and the manner of subdivision of both muscles; and absence of one or other of them has been recorded. Most commonly each muscle divides into two parts, anterior and posterior in position, though sometimes the division is only indicated by grooves and sometimes is complete to the bases; when the division is complete the opposed surfaces are reciprocal in form, a convex surface of the one (usually the anterior) fitting a concave surface of the other. The **chordæ tendineæ** are fewer in number and stronger than those of the right ventricle. They arise from the apices of the papillary muscles, and not infrequently also from their sides, and run upwards in the intervals between the cusps to be attached to the adjacent margins of both of them. Those of the second order do not reach so far upwards on the aortic cusp as on the posterior cusp, so that the greater part of the ventricular surface of the aortic cusp is much smoother than the same surface of the other cusps; naturally, also, chordæ tendineæ of the third order are not found on it.

The "outflowing" part of the left ventricle is bounded laterally by the aortic cusp of the mitral valve and by the two papillary muscles and medially by the smooth septum. It is much shorter and is less arched than the corresponding part of the right ventricle. The walls of that part of it which adjoins the root of the aorta (aortic vestibule, SIBSON) are fibrous, or at one part even fibro-cartilaginous (p. 68), so that during systole of the heart its cavity remains unobliterated.

The aortic orifice is on the same plane as the mitral orifice, and lies in front of it and on its medial side: it is, on an average, 75 mm. in circumference in the male and 68 mm. in the female (see p. 123).

The Development of the Ventricles.—The developmental history of the ventricles and of the atrio-ventricular and arterial valves is considerably complicated, for separate processes occur at the same time in the different parts of the common bulbo-ventricular chamber and effect the subdivision of these parts independently of one another into right and left cavities; and only at

a later period do the different septa which are formed fuse with one another to form a complete bulbo-ventricular septum. Some reference must also be made here to the changes in the heart wall.

There is at first, as has been stated (p. 14), a considerable distance between the endothelial tube and the myo-epicardial mantle along the whole length of the primitive heart, and occupying the interval there is during life a serous fluid which in prepared sections appears as a fibrillated, cell-free, coagulated mass; MALL has stated, however, that the fibrillæ are processes of the endothelial cells. At a later period nuclei are to be seen in the coagulum close to the endothelium. The space between the endothelium and the myo-epicardium disappears first in the sinus, then in the atrium, and lastly in the ventricle, and the two layers come into close contact in these parts; in the atrial canal and the bulbus cordis, however, endocardial swellings, very comparable in appearance to Wharton's jelly, are developed and fill the earlier cell-free space. In the myo-epicardium the epicardium is differentiated at an early period as a covering layer, one cell thick, on the surface. The **myocardium** itself differentiates first in the ventricle where trabecular ridges appear on the inner surface and, covered on all sides by the endocardium, run more or less freely through the cavity; the trabeculæ appear first at the apical part of the ventricle and advance towards the atrial canal and the bulbus cordis. The ventricular muscle now consists of two layers, a thin outer cortical layer and a thick inner trabecular layer. In the cells of the trabecular part longitudinal fibrillæ make their appearance, first near the surface of the cell and later in its central parts; and soon they can be seen to extend from one cell to another and can ultimately be followed in a longitudinal direction over several cells. The cardiac myoblasts thus early form a syncitium, the junction between the cells taking place at their ends; the side boundaries of the cells always remain distinct. This differentiation occurs much later in the cortical layer. On the bulbus the myocardium reaches up to the attachment of the pericardium, that is to the place of transition from the bulbus to the truncus arteriosus; at a later period this boundary cannot be accurately defined, for the myocardium on the distal part of the bulbus disappears even before it is differentiated into recognisable muscle tissue. This retrogression of the bulbar myocardium is a significant feature of all vertebrate hearts; it is probably to be related to the replacement of a muscular sphincteric control of the exit tube from the heart by a purely mechanical valvular control.

The Atrial Canal and the Atrio-Ventricular Valves.—The atrial canal, as has been described (p. 19), becomes oval in shape, its long axis being placed transversely, and it occupies a position in the centre of the floor of the atrium, so that the lower border of the septum primum reaches it at its middle and divides it, from above, into equal parts; and at this time it becomes surrounded on all sides by the expanding atria and ventricles, so that in longitudinal section of the heart it appears telescoped within the cavity of the ventricle (fig. 13). Its lumen is narrowed and becomes slit-like by the development of the subendocardial tissue in its wall (see above). This tissue forms marked swellings on its anterior (upper) and posterior (lower) walls (fig. 28); these swellings are usually known as the anterior and posterior **endocardial cushions**. At the ends of the canal the swellings are much smaller (fig. 38). The trabecular formations of the ventricle, advancing towards the atrial canal, now undermine the endocardial cushions and these project, therefore, with free, plump, rounded edges into the ventricular cavity and constitute the rudiments of the **atrio-ventricular valves**. The undermining process continues to the upper ends of the cushions which, in the end, are attached only by their bases. The primary cusps are thus purely

endocardial structures; and attached to their ventricular surface are the ventricular trabeculæ which have undermined them. The anterior and posterior endocardial cushions now fuse along a considerable part of their transverse length so that the two atrio-ventricular openings, which are thus defined, represent the end parts of the original slit-like lumen and are separated from one another by the width of the fused zone. Up till this period the atrial and ventricular musculatures are continuous with one another through the musculature of the atrial canal, but this continuity is now interrupted by the ingrowth of a wedge-shaped zone of fibrous tissue in the atrio-ventricular furrow. The apex of this wedge grows more and more towards the heart lumen and completely separates the cortical ventricular muscle from the atrial muscle; the process is, of course, a retrogression of the musculature of the atrial canal, and it occurs round its whole circumference except over a small region on the back of the canal where the muscle persists as the atrio-ventricular bundle of HIS (see further, p. 96). There is now a cortical sino-atrial musculature and a cortical ventricular musculature which are unconnected except by the bundle of HIS, but the trabecular musculature is still free of this division, and at the insertions of the atrio-ventricular valves the atrial part is continuous with the ventricular part. The atrial trabecular muscle fibres are now to be found growing into the atrio-ventricular cusps; how far this is an active invasion and how far simply the result of the further undermining of the wall of the atrial canal by

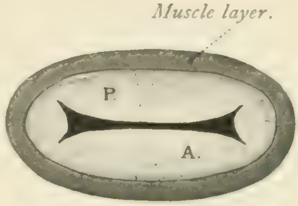


FIG. 38.—A DIAGRAM OF A TRANSVERSE SECTION THROUGH THE ATRIAL CANAL.

P.A., posterior and anterior endocardial cushions; the dotted lines indicate the line of fusion of the septum primum.

FIG. 39.—DIAGRAMS TO ILLUSTRATE THE DEVELOPMENT OF THE ATRIO-VENTRICULAR VALVES AND CHORDÆ TENDINEÆ.

the ventricular trabeculæ is not yet decided, but in the cusps the atrial fibres retain their connection with the ventricular trabeculæ. The cusps may be described, therefore, to have reached a secondary condition for they now consist of muscle tissue in addition to the original endocardial tissue. The retrogression of the musculature of the atrial canal continues and the musculature of the cusps is replaced by fibrous tissue which is continuous with the apex of the wedge-shaped ring which previously had interrupted the cortical musculatures; the sino-atrial trabecular muscle is thus completely separated from the ventricular

trabeculæ. Similar changes occur in the distal parts of the ventricular trabeculæ to produce the chordæ tendineæ. The valvular apparatus is virtually completed at the eighth week.

The atrio-ventricular valves are thus formed partly from the endocardial cushions and partly from the undermined muscular wall of the atrial canal; the boundary between the two parts, however, cannot be accurately indicated, though the noduli of Albini (p. 44) probably represent localised persistences of the original succulent endocardial tissue. The lower edges of the cusps represent the distal boundary of the atrial canal and as such they may be taken to define the morphological boundary between the atria and the ventricles in the adult. The retrogression of the musculature of the atrial canal represents the disappearance of the original muscular sphincter guarding the orifice between the atria and the ventricles, its place being taken by mechanically acting fibrous valves.

The Development of the Ventricular Septum.—The formation of the ventricular septum begins after the atrial septa are well defined. It appears first as a ridge (septum inferius, His) in the apical part of the common ventricle, and corresponds in position with the furrow which is seen there on the outer surface (fig. 14). The ridge gradually grows upwards towards the atrio-ventricular and bulbar orifices forming a more and more complete septum, and the right and left ventricles are more and more completely separated from one another; for a considerable period, however, the two chambers are connected with one another over the upper free edge of the septum by the **interventricular foramen**, but this is gradually narrowed and at last disappears, the closure being effected, in man, by a membranous structure which forms the **pars membranacea septi** of the complete septum (p. 55). The cavity of the left ventricle is at first of greater size than that of the right, and remains so even in a fœtus of 175 mm. C.R length; by the more rapid expansion of the right ventricle, following the inclusion in it of the proximal part of the bulbus, the two cavities later become of equal size.

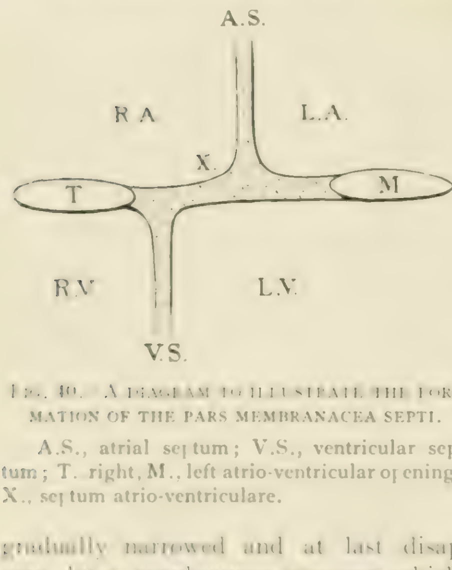


FIG. 40. A DIAGRAM TO ILLUSTRATE THE FORMATION OF THE PARS MEMBRANACEA SEPTI.

A.S., atrial septum; V.S., ventricular septum; T. right, M., left atrio-ventricular opening; X., septum atrio-ventriculare.

The process of the closure of the interventricular foramen requires a more extended description, especially in man. The upper end of the posterior (or lower) edge of the ventricular septum advances along the posterior wall of the ventricle towards the atrial canal and ultimately reaches the posterior endocardial cushion with which it fuses near its right end (fig. 28); that is, the upper edge of the septum is not placed below the middle of the atrial canal and opposite the lower edge of the septum primum of the atrium, but is placed at the right end of the fused parts of the anterior and posterior endocardial cushions. The anterior (or upper) edge of the ventricular septum, ascending on the anterior wall, passes into and becomes continuous with the anterior end of the remnant of the fold of the bulbo-atrial groove, but does not pass into the bulbus. In the bulbus there is formed, as is described below, a septum, named the proximal

bulbar septum, which divides the cavity of the bulbus into two parts. The lower free concave edge of this septum grows downwards towards the ventricle; its anterior prolongation fuses with the anterior prolongation of the ventricular septum, while its posterior prolongation broadens at its lower end and fuses with the right part of the anterior endocardial cushion of the atrial canal. The interventricular foramen at this stage has, therefore, the following boundaries: below and in front there is the concave upper edge of the ventricular septum; this is continued forwards and upwards into the lower edge of the proximal bulbar septum which forms the upper boundary of the front part of the foramen; the upper boundary of the back part of the foramen is formed by the fused endocardial cushions of the atrial canal. The endocardial cushions of the atrial canal, already fused with one another, now fuse near their right ends with the back part of the ventricular septum and thus close the back part of the interventricular foramen, while, at a later period, the anterior endocardial cushion fuses with the front part of the septum and closes the front part of the foramen; and there is thus formed the pars membranacea septi, the bulbar septum taking no part in its formation. The closure of the foramen thus takes place under the right part of the common atrio-ventricular orifice: the right orifice is, therefore, close to the septum, while the left orifice is some distance (the width of the fused parts of the anterior and posterior endocardial cushions) from it. (For further details of this process, see FRAZER.) Now, since the atrial septum reaches the middle of the upper side of the fused cushions and the ventricular septum reaches the right end of the under side, a part of the fused cushions (x, fig. 40) intervenes between the right atrium above and the left ventricle below; this part gradually turns into the same plane as the atrial and ventricular septa and is known as the atrio-ventricular septum (HOCHSETTER) or the upper part of the pars membranacea septi (see p. 55).

The Development of the Bulbar Septa and of the Arterial Valves.—There are three independent septa formed in the common exit tube of the heart: (1) One, the **aortico-pulmonary septum**, in the truncus arteriosus (the extra-pericardial part of the exit tube); this begins distally and grows towards the heart and separates the systemic aorta from the pulmonary artery. (2) and (3) Septa which develop in the distal and proximal parts of the bulbus and are known as the **distal** and **proximal bulbar septa**. These three septa are formed at the same time as the septa of the atrium, with the division of which the division of the exit tube is associated in phylogeny.

The bulbus cordis, as already described (p. 19), is absorbed partly into the truncus, of which it forms the intra-pericardial part, and partly into the ventricles, chiefly the right ventricle (fig. 15); and it may be here noted, that imperfect absorption of the lower part of the bulbus is the commonest abnormality of the heart (p. 126). The boundary between the two parts of the bulbus lies along the attached edges of the arterial valves. In the distal (truncus) part of the bulbus the subendocardial tissue forms at first a uniformly thick ring, but later four endocardial ridges [1] project into the lumen; at the distal end, and commencing on the right side and passing to the left on the posterior surface, these ridges are numbered (after BOAS) 1, 2, 3, and 4 (fig. 41). In a distal direction these ridges gradually taper away into the truncus, the aortico-pulmonary septum of which has not yet reached its lower end; in a proximal direction they run in a spiral course,[2] ridge 1 passing posteriorly and to the left, and ridge 3 anteriorly

[1] The endocardial ridges, typically four in number but sometimes, as in the atrial canal, reduced to two, are the primitive valvular apparatus of the heart.

[2] The spiral course of the bulbar ridges is, to the writer, evidence of the original looping of

and to the right. These two ridges (1 and 3) continue their growth into the lumen of the bulbus and, fusing with one another across the tube, form the distal bulbar septum which is transversely placed at its upper end and in an oblique antero-posterior plane at its lower end. At a later stage the advancing lower concave edge of the aortico-pulmonary septum fuses with the upper edge of the distal bulbar septum and completes the separation of the intra-pericardial parts of the aorta and pulmonary artery, but for some time these vessels communicate with each other between the edges of the septa.

In the proximal (ventricular) part of the bulbus the endocardial thickening is irregular and two ridges project into the lumen. These thickenings (*Wälzle*, A and B of BORN) run spirally round the tube, ridge A commencing on the left side above and running forward to the front of the lower end and on to the anterior wall of the ventricle (see above), and ridge B commencing on the right side above and ending on the anterior endocardial cushion below. These ridges are undermined from below by the ventricular trabeculæ as more and more of this part of the bulbus is included in the ventricles; they become, therefore, shorter and shorter. In a distal direction they continue to extend, ridge A winding on to the back of the lumen and ridge B on to the front, and they meet and ultimately fuse with the lower end of ridges 1 and 3 of the distal bulbar group, ridge A fusing with ridge 1 and ridge B with ridge 3. The aorta and pulmonary artery are thus completely separated from one another and owing to the spiral course of the septa (fig. 41) the two vessels are spirally twisted on one another. The separation of the walls of the two vessels is accomplished by the ingrowth of the connective tissue of the aortico-pulmonary septum into the endocardial ridges. The undermining of the proximal part of the bulbus continues, and ultimately it becomes included as the conus of the right ventricle and aortic vestibule of the left ventricle; while at first, therefore, the aorta and the pulmonary artery arise by relatively long parts from the ventricles, and the distance between insertion of the semilunar cusps and the ventricular septum is relatively great, in the newborn these parts are very much shortened. After the division of the distal part of the bulbus, each of the two vessels contains one half of ridges 1 and 3, and the pulmonary artery also ridge 2 and the aorta also ridge 4. The peripheral ends of these ridges become more and more flattened and ultimately disappear, but the proximal ends increase in size and become hollowed out from the distal side to form the primitive semilunar valves. These are at first thick succulent endocardial formations, but with the encroachment of the fibrous tissue of the truncus and the disappearance of the myocardium they undergo fibro-tendinous changes and appear as in the newborn. The bulging of the walls of the vessels opposite each cusp takes place soon after the cusps are defined to form the sinuses of Valsalva. The cusps opposite the septum between the arteries are the last to develop, that is the cusps from ridges 2 and 4, and, as already indicated (p. 48), they may be double or deficient.

FIG. 41.—A DIAGRAM OF THE BULBAR SEPTA. (The explanation is in the text.)

the primitive cardiac tube, and cannot be accounted for if the chambers of the heart are considered to be only diverticula of the tube. The same spiral course is found in Elasmobranchii and is even greater in Dipnoi (GRAHAM KERR).

THE FORM OF THE SYSTOLIC HEART

The descriptions of the heart given so far are of the diastolic or relaxed heart. It is not possible, of course, to record all the changes of heart form which occur during the cardiac cycle, yet some description may be made of the form of the systolic or fully contracted heart. It is to be noted, however, since the heart cannot be fixed with certainty in its systole, that the descriptions given here refer to hearts fixed by technical methods to imitate the systolic heart as nearly as possible. The most suitable and useful methods are by the use of heat (as introduced by Hesse in his work on the dog and subsequently used by Krehl and Keith on the human heart), which produces a uniform shortening of the muscle fibres; and they should be used, as injections of boiling water or of hot wax, while the heart is *in situ* and without disturbance of any of its connections, for these probably play a large part in the form affected by the contracted atria. It is supposed, of course, in the use of these methods that all parts of the living myocardium contract synchronously and that the heat contraction will bring about a shortening of the fibres of the same amount as occurs in the normal contraction. The former of these suppositions is, of course, incorrect and the latter almost surely so, yet there is a formal similarity with the functional condition and it is, therefore, described as the contracted heart; and in many respects the conclusions which have been reached have been confirmed by studies on the living (animal) heart.

The changes in the **external form** of the heart from diastole to systole have not yet been adequately studied. The descriptions which have been given are largely based on naked-eye observations; and that such are not to be relied on is evident, for example, in the old controversy as to whether the heart is shorter or longer during systole. Galen believed that the heart was longer in systole, a view which was also taken by Vesalius, Riolan, Borelli, and others; but, according to Harvey, the lengthening is only a relative one, for in the systolic heart all the dimensions are decreased, but the length least of all, and in this description Lower, Stenson, Lancisius, Winslow, Senac, Haller, Ludwig, and Winkler have agreed.

Hesse, working on hearts contracted by heat, describes the form of the ventricular part of the systolic heart to be conical and states that both transverse measurements of the base (the atria and the aortæ being removed) are decreased compared with the measurements of the diastolic heart, but that the distance from the apex of the heart to the plane of the atrio-ventricular orifices is not shortened.[1] The following changes on the surface of the heart have been described: (*a*) The conus arteriosus becomes shorter and, as Krehl points out, this shortening certainly gives the impression that the whole heart is shortened. (*b*) The anterior longitudinal sulcus is deepened and becomes S-shaped in curvature by the lower part of left ventricle advancing itself over the right ventricle (Hesse, in the dog). If this observation be correct then the rotation of the heart in systole comprises two factors, a rotation of the whole heart and a distortion of the heart itself; and that it is so appears to be confirmed, for Braun, from the examination of kinematograph records of the contracting heart, has described the appearance of a protuberance (a "heart-humping") on the left ventricle above the apex which remains throughout the whole of systole. It is this area of the heart which rests on the anterior chest wall during the "apex beat."

[1] The ventricular base is drawn backwards towards the atria in systole.

The diminution in the size of the **cavities** of the **ventricles** in systole must be brought about by a rearrangement of the muscle volume bounding them, since the volume itself cannot be changed in contraction. If, therefore, the long measurement of the heart remains the same throughout the whole cardiac cycle, then, since the volume remains the same, the area of a transverse section of the heart musculature will be the same in systole as in diastole, as indeed HESSE has proved with the planimeter. Now since in the systolic phase of the

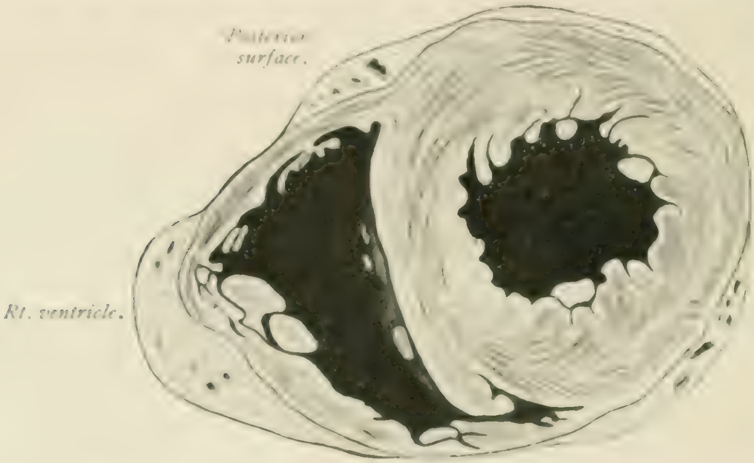


FIG. 42A.—CROSS SECTION OF THE VENTRICLES IN THE DIASTOLIC HEART.

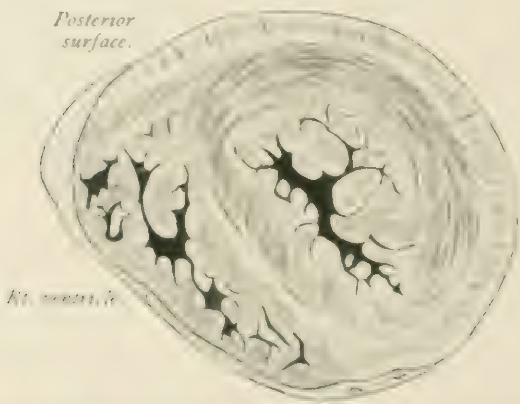


FIG. 42B.—CROSS SECTION OF THE VENTRICLES IN THE SYSTOLIC HEART.

heart "the muscle-ring" of a transverse section must be lessened without its area being diminished, it follows, as KREHL and STARKE have shown to happen, that the inner boundary of the ring must become smaller to a greater extent than the outer boundary, and there will be produced an approximation of the inner layers of the heart, as is shown in the formation of longitudinal ridges. The arrangement of the heart musculature, however, is not concentric, but is of such a kind that the side walls are thickened and are approximated to the septum (see p. 71); the resulting conditions, therefore, will differ in the right and left ventricles. In the contracted **left ventricle** the meshes between the trabeculæ are obliterated and the trabeculæ are more prominent. The two papillary muscles

come into contact with one another and the lateral wall of the ventricle comes into contact with the papillary muscles, so that the inter-papillary space and the "inflowing" part of the ventricle, with the exception of a small space between the posterior cusp of the mitral valve and the heart wall, are obliterated. At the junction of the anterior wall with the septum a prominent longitudinal ridge is developed which fills the space which is found there in the diastolic heart; and a second flatter ridge is to be seen on the septum itself reaching up to the semilunar valves, for the right and anterior of which it serves as a prop (KREHL). (Similar ridges are described by HESSE in the dog and by ALBRECHT in the sheep.) The uppermost part of the "outflowing" part of the ventricle (aortic canal, SÉE), bounded by the aortic cusp of the mitral valve and the septum, is constricted by these longitudinal ridges, and as is emphasised by HESSE and KREHL its lumen is then smaller than that of the commencement of the aorta. The base of the heart being smaller in all its dimensions, as already described, the atrio-ventricular opening is narrowed; this happens chiefly in the transverse direction, the lateral circumference of the annulus advancing to the aortic wall. In the **right ventricle** the free lateral wall carrying the anterior papillary muscle is approximated to the septal wall, and in the apical part of the heart the cavity is obliterated by the apposition of the trabeculæ. The crista supraventricularis projects more deeply into the lumen of the ventricle and the trabecula septo-marginalis (moderator band) is contracted, so that the separation of the "inflowing" and "outflowing" parts of the cavity is more sharply defined than in the diastolic heart. Of the "inflowing" chamber there remains in the systolic heart only a part of the perivalvular groove and a small central supra-papillary space near the heart base. The atrio-ventricular orifice is narrowed. The "outflowing" chamber is reduced in size and becomes of a tubular form, but it is not so much reduced as the outgoing chamber of the left ventricle; so that in the systolic heart the amount of blood left in the right ventricle is greater than the amount left in the left ventricle. It is thus explained that although the capacity of the right ventricle is greater during diastole the same quantity of blood is expelled from the two sides.[1]

The changes in the **external form** of the **atria** are (1) the interatrial groove on the upper and posterior walls and the sulcus terminalis on the right atrium are deepened; (2) the atrial appendages are raised a little so that they more directly face the atrio-ventricular openings; and (3) on the roof of the left atrium a frontally placed furrow is formed between the upper pulmonary veins and the left appendix. The changes in the **interior** of the atria [2] are directed to the closing of the mouths of the great veins to prevent the regurgitation of blood into them during systole. In the **left atrium** there is at least the anatomical possibility that the pulmonary veins may be closed by the sphincter-like muscle fibres which surround their orifices and extend along their intra-pericardial parts (p. 71), but whether they are so closed yet remains to be conclusively stated; KEITH believes that they are closed by an approximation of the anterior and posterior walls. In the **right atrium** there is no such possibility, and the mechanisms for closing the venæ cavæ are other than sphincteric contraction. The musculi pectinati become closely applied to one another. The crista terminalis is powerfully contracted, its radius of curvature is much shortened, and it projects downwards as a shelf into the atrium. The limbus fossæ ovalis is shortened

[1] The old discussion of the relative size of the ventricles is fully given in TODD'S "Encyclopædia."

[2] KEITH believes that to produce the changes of the atrial walls the contraction of the right crus of the diaphragm is a necessary factor.

and thickened, its anterior part being drawn backwards. The separation between the sinus venarum and the atrium thus becomes more pronounced, and, according to KEITH, the two parts are separated from one another. The torus Loweri becomes very prominent and between it and the crista terminalis above, and between it and the margin of the Eustachian valve below, there are formed narrow, deep, transversely placed, slit like clefts into which the venæ cavæ open and in which their orifices are almost obliterated; and in the lower cleft the lower part of the fossa ovalis is hidden (fig. 13). The angulation between the two cavæ is increased. The sub-Eustachian sinus becomes a deep fossa, bounded medially by the Eustachian valve. The coronary sinus is closed by the approximation of its septal wall (anterior limbic band) and its valvular fold (KEITH).

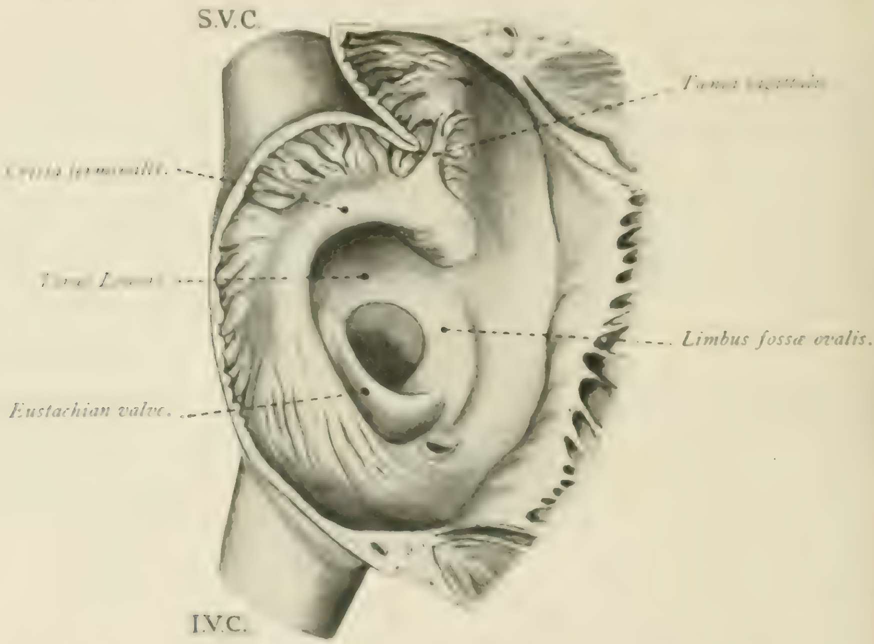


FIG. 13.—THE INTERIOR OF THE RIGHT ATRIUM IN THE CONTRACTED STATE. (After KEITH.)

In the **left atrium** the changes are much simpler. A ridge (tænia terminalis sinistra, KEITH), almost circular in its extent, frontally placed, and corresponding to the groove previously mentioned, appears in the roof of the atrium and projects well into its cavity and divides it into anterior and posterior parts. The posterior part (vestibule, KEITH) is a small transversely placed chamber into the lateral parts of which the pulmonary veins open, but the separation between it and the anterior part (atrium proper) is by no means so marked as in the right atrium.[1]

THE STRUCTURE OF THE HEART

The heart wall consists chiefly of muscle tissue which is known as the **myocardium**. This is invested on the outer surface by a serous membrane, the **epicardium** (p. 25), while on its inner surface, that is, in the cavities of the heart, it is lined with **endocardium** (p. 26); both of these layers have already

[1] KEITH, however, describes the separation to be complete.

been described and it remains now to describe the arrangement of the musculature.

The Myocardium.—Cardiac muscle differs from skeletal muscle not only in its microscopic characters, but also in some of its macroscopic arrangements; and there is much less fibrous tissue in it than in skeletal muscle. Of the microscopic differences, as are described in Vol. II., Part I., it is necessary to note here only that heart-muscle cells are arranged in a general syncitial network (fig. 44), the fibrils being common to more than one cell; the presence or absence of cement lines (*Kittlinien*) as cell boundaries does not affect the general statement. The muscle cells are arranged in bundles which do not show the distinct definition of skeletal muscle bundles, for they anastomose with one another through numerous lateral branches and, as it were, reproduce in a grosser form the finer syncitial arrangements of the cells. These bundles can be followed for considerable lengths in practically any vertebrate heart, especially when the arrangement of the musculature is simple; and the interchange of fibres at the sides of the bundles can readily be observed. The anastomoses between the bundles thus being chiefly in one plane, the bundles are bound to one another in layers or sheets which may be only in loose union with the layers which lie superficial and deep to them. These layers can be defined most easily on the atria and on the outer and inner surfaces of the ventricles. Even here, however, their isolation demands the division of a certain amount of anastomoses between the layers, and to this extent, therefore, they must be considered artefacts though they represent the direction in which the muscle shortens in contracting. In the middle parts of the muscle substance of the ventricles the layer formation in the same sense no longer exists since the anastomoses are developed more equally in all directions. In certain parts, for example in the papillary muscles, the anastomoses are so uniformly developed that the muscle bundles cannot be isolated from one another; yet even here there is a principal direction in which the bundles are arranged.

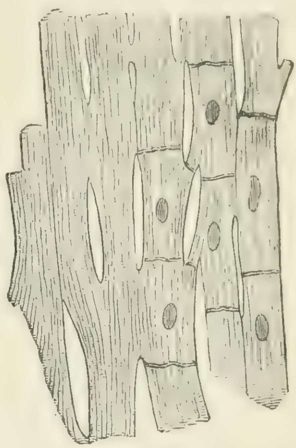


FIG. 44.—MUSCULAR FIBRES FROM THE HEART, MAGNIFIED, SHOWING THEIR CROSS STRIÆ, DIVISIONS, AND JUNCTIONS. (SCHWEIGGER-SEIDEL.)

The nuclei and cell-junctions are only represented on the right-hand side of the figure.

VESALIUS was the first definitely to teach that the heart wall consists of interwoven muscle fibres arranged in layers; before him the heart wall was described to be formed of a "special parenchyma" which was not muscle tissue, and GALEN at some length points out the differences.

There are in the atria of the adult heart moderate numbers of small elastic fibres among and lying parallel to the muscle fibres; apparently they are not present at birth, but are very much increased in number and size in old age. There is much less elastic tissue in the ventricular myocardium.

The Heart Skeleton.—The cardiac musculature is attached to fibrous and fibro-cartilaginous parts which lie at the junctions of the atria and the ventricles and the ventricles and the arteries and at the apices of the papillary muscles, and may well be named, as seems first to have been done by French writers, the heart skeleton. The heart skeleton consists of the following parts (figs. 45 and 46): (1) The **septum membranaceum**, the position of which has already been described (p. 55). It remains now to refer to its continuation upwards

in front into the right spatium intervalvulare to reach the " aortic root " where it is continuous with the " tendon of the conus " (see below), and to its extension backwards and upwards as the septum atrio-ventriculare (p. 55) into the trigonum fibrosum dextrum. (2) The **trigonum fibrosum dextrum** (posterior aortic ligament, MALL) is a mass of fibrous tissue of almost cartilage-like consistency [1] which lies behind the aortic orifice and extends backwards in a more or less pointed process between the two atrio-ventricular orifices. As seen from above (fig. 46) it has approximately a triangular shape. Anteriorly it is bounded by the aortic wall and is directly continued into the fibrous aortic root on the left and right sides. The posterior pointed process (filum coronarium medium, HENLE) forms the medial boundary of the left atrio-ventricular orifice and is continued into the annulus fibrosus of that opening, and from its right margin part of it is continued into the thin annulus fibrosus of the right atrio-ventricular opening. The septum membranaceum (septum atrio-ventriculare) is continued upwards into the right margin of the trigone, and the tendon of Todaro (p. 33)

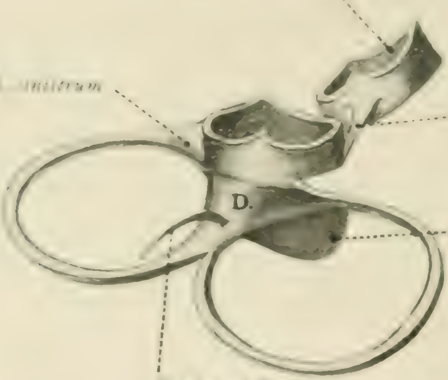


FIG. 45.—THE HEART SKELETON. (After UNGAR.)
D, trigonum fibrosum dextrum.

is also attached to it here. On the left, in front, it is continued into the left trigonum fibrosum, the aortic cusp of the mitral valve arising from the adjacent parts of the two trigona. Close to its attachment to the aorta it is perforated by the atrio-ventricular bundle of HIS. (3) The **trigonum fibrosum sinistrum** (left aortic ligament, MALL), smaller than the right but of the same cartilaginous consistency, lies on the left side of the aortic orifice. The wall of the aorta forms its concave base, while its apex passes to the left and is continued as a pointed process (filum coronarium sinistrum, HENLE) round the front of the left atrio-ventricular opening and into its annulus fibrosus. The left anterior angle is continued directly forwards into the aortic root. (4) The **conus tendon** of KREHL (right aortic ligament, MALL; septum aorticum superius, HIS) is a strip of tendinous-like fibrous tissue which begins opposite the anterior aortic cusp and runs forwards, to the left, and upwards in the roof of the conus of the right ventricle to the root of the pulmonary artery, where it ends in the posterior spatium intervalvulare (fig. 46). It does not extend, however, through the whole thickness of the conus musculature. It was first described by KREHL

[1] It is often referred to as the central cartilage of the heart.

in the dog; MacCallum afterwards described it in the pig, and Mall in the human subject. Along it the conus and the aorta are firmly blended. When followed downwards it leads to the membranous septum. (5) The **arterial roots**, the fibrous tissue rings at the roots of the pulmonary artery and aorta, have already been described (p. 49). It remains, however, to indicate here that the aortic root is fixed at the heart base to the right trigonum fibrosum behind, to the left trigonum fibrosum on the left, and to the conus tendon on the right (fig. 45); and that in this sense these parts have been well named by Mall the "aortic ligaments," which so tie the aorta to the heart that the force of contraction is prevented from "shooting the aorta out of the heart" (Mall). (6) The **annuli fibrosi** of the atrio-ventricular openings, the first parts of the heart skeleton to be recognised and described, consist of the fibrous tissue which surrounds these orifices. It is to be noted, however, that at neither opening is

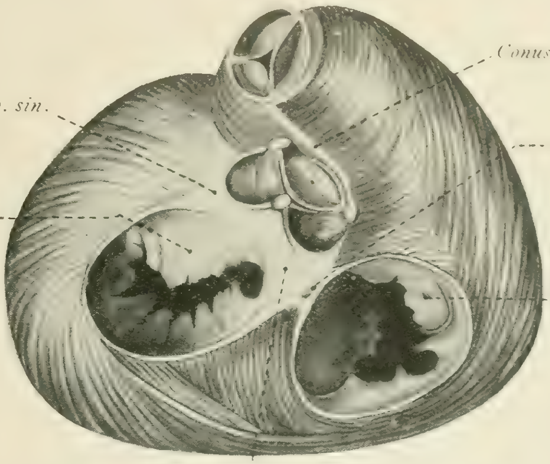


Fig. 46.—The heart skeleton.
A view of the base of the ventricles after removal of the atria.

there a uniformly developed ring-like band, but, as Henle first indicated, each annulus consists of parts of very different consistency and structure. The right annulus consists of the dense right trigonum fibrosum which forms its left circumference and is continued forwards and backwards into the loose fibrous-tissue zone which encircles the remainder of the orifice; at certain parts this zone is very thin and almost loses its definition, its position then being indicated by the attachments of the cusps of the tricuspid valve (fig. 46). The left annulus consists of the adjacent portions of the trigona fibrosa and of the fila coronaria (medium and sinistrum) which pass from them; but at its left and posterior parts it consists of loose tissue, forming, however, a more distinct band than on the right side (fig. 46). The aortic root may be described as forming that part of the annulus which lies between the trigona.

Histology of Heart Skeleton.—The structure of the heart skeleton differs at different parts and also at different ages. The annuli fibrosi proper consist of loose fibrous tissue in which there are small fatty patches. The septum membranaceum consists of interlacing bundles of dense fibrous tissue; on both surfaces there are abundant elastic fibres, but these belong to the endocardium with which it is covered. The trigona are more complex in structure. They have

been said to consist of fibrocartilaginous tissue (Dogiel, Pretolani) and the presence of cartilage cells has been affirmed (Luschka, Podhzer). Favaro describes them to be formed of a reticulated fibrous tissue, and Retterer and Lelièvre of a vesiculated fibro-elastic tissue (the last authors have described the development of the tissue and the different end forms in different animals). The tissue seems to have a special affinity for hæmatoxylin and is very dark in stained sections, especially in children. It is not coloured uniformly with Van Geison stain, yellowish patches of varying size appearing in the red background; at these parts large cells with well-defined nuclei are present, while in the red parts the cells are small and few in number. The elastic tissue is small in amount; in the child's heart it is absent.

The structure of the heart skeleton varies in different animals. The os cordis in the trigonum fibrosum dextrum of the ox and sheep is one such variation; it reaches downwards into the upper part of the pars membranacea septi and is easily felt from the right atrium. True cartilage is to be found in this position in the horse, and sometimes a smaller cartilage in the left trigonum; these cartilages are also to be found in the pig. In old age, in man, calcification to a considerable extent may occur.

The Atrial Musculature. The atrial musculature is much more simply arranged than the ventricular musculature. It was first described in detail

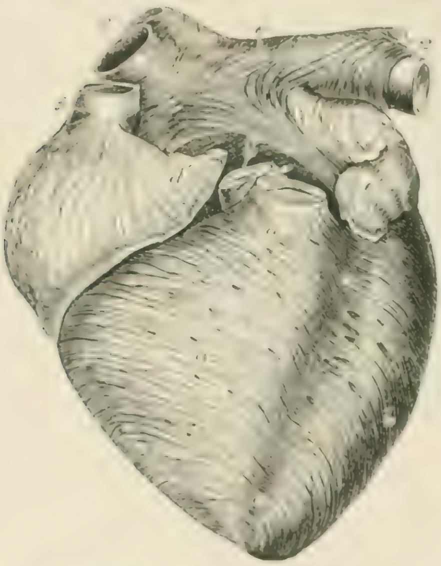


Fig. 47. Anterior view of heart of a young subject dissected after long boiling, to show the superficial muscular fibres. (Allen Thomson.) ½.

This figure is planned after one of Luschka's, but its details were chiefly taken from an original preparation. The aorta, *b′*, and pulmonary artery, *a′*, have been cut short close to the semilunar valves, so as to show the anterior fibres of the atria. *a*, superficial layer of the fibres of the right ventricle; *b*, that of the left; *c*, *c*, anterior interventricular groove; *d*, right atrium; *d′*, its appendix, both showing chiefly perpendicular fibres; *e*, upper part of the left atrium; between *e* and *b′*, the transverse fibres which behind the aorta pass across both atria; *e′*, appendix of left atrium; *f*, superior vena cava, around which, near the atrium, circular fibres are seen; *g*, *g′*, right and left pulmonary veins with circular bands of fibres surrounding them.

by Gerdy and has since been specially studied by Bourgery, Luschka, Keith, Favaro, and Papez. A dissection from the surface displays two groups of fibres, namely (1) longer superficial fibres which are common to both atria, and (2) shorter deep fibres proper to each atrium. The superficial fibres on the whole run transversely, while of the deeper fibres some form vertical loops and others annular bands round the atrial orifices. Both sets of fibres, however, show considerable individual variations. The wall of the left atrium is thicker and more muscular than that of the right atrium.

1. Among the **long fibres** which are common to both atria the following specific bundles may be described. (A) The fasciculus interatrialis horizontalis (Luschka) which is moderately constant in its course and extent though it is variable in size. It emerges from the posterior interatrial sulcus near the coronary sulcus, its fibres being attached to the annuli fibrosi, especially the annulus of the left side (fig. 48); and it passes to the left on the posterior surface of the left atrium and then forwards to the base of the atrial appendix. It divides there into two parts, one passing below and one above the appendix. That part which passes below the appendix is joined by a small part of that

which passes above and is then continued over the anterior interatrial furrow to the surface of the right atrium on which it runs laterally in front of the superior vena cava and may be traced along the medial surface of the right appendix (fig. 47). The remaining part of the fasciculus, that which passes above the left appendix, in part dips into the anterior interatrial furrow and ends in the septum (tænia terminalis sinistra, KEITH) and in part crosses the furrow and passes behind the superior vena cava. (B) The fasciculus interatrialis verticalis (LUSCHKA) runs almost at right angles to the fasciculus horizontalis. It appears from behind the aorta, ascends over the anterior surface of the left atrium, and then passes between the right and left pulmonary veins to the posterior surface where the greater part of it disappears into the posterior interatrial furrow; a smaller part is continued on to the right atrium and reaches as far as the posterior wall of the inferior vena cava, and LUSCHKA has described (in one instance) its attachment there to the diaphragm.

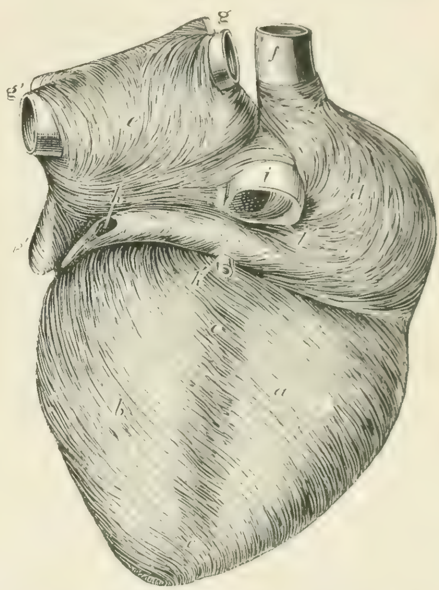


FIG. 48.—POSTERIOR VIEW OF THE SAME PREPARATION AS IS REPRESENTED IN THE PRECEDING FIGURE. (ALLEN THOMSON.) $\frac{2}{3}$.

a, right ventricle; *b*, left ventricle; *c*, posterior interventricular groove; *d*, right atrium; *e*, the left; *f*, superior vena cava; *g*, *g'*, pulmonary veins cut short; *h*, coronary sinus, with cardiac muscle fibres in its wall; *h'*, middle cardiac vein joining the coronary sinus; *i*, inferior vena cava; *i'*, Eustachian valve.

2. The **short fibres** are arranged in distinct bundles only at certain parts of the atria, at the other parts, where the walls of the atria are thinner, the arrangement is indefinite and subject to considerable variation; in a general way they may be described to form vertical looped fibres, which arch over the atria and are attached at their ends to the atrio-ventricular skeletal rings and circular horizontal fibres. The following bundles are among those which can be defined. (A) Circular fibres, forming sphincter-like bundles, are quite distinct round the pulmonary vein orifices (fig. 47) and extend along the pulmonary veins as far as the pericardium; in man the extrapericardial parts of the pulmonary veins do not contain cardiac-muscle fibres as has been described by RÄUSCHEL, STRIDA, and FAVARO, though they are to be found in these parts in other forms (rat, MACKENZIE). There are no comparable sphincteric bands round the orifices of the venæ cavæ. At the lower caval orifice the transition from the atrial to the venous wall is sharply defined (fig. 47), and at the upper orifice, though a few atrial fibres [1] are prolonged on the vein wall in a spiral manner, they cannot have any sphincter-like action; a special band of atrial fibres is described by KEITH in the septal wall of the superior orifice. (B) The orifice of the coronary sinus is surrounded by circular fibres which also extend along the sinus as far as the valve of Vieussens in its interior (fig. 47). (C) The musculi pectinati consist of almost parallel bands which pass laterally from the

[1] KEITH regards these fibres as persistent sinus musculature.

crista terminalis and end at the coronary sulcus in the annulus dexter. (D) The orifice of the left atrial appendage is constricted and defined by a weakly developed circular band; but there is no corresponding band at the orifice of the right appendage. (E) A dissection of the inner surface of the right atrium displays a series of distinct bundles which have a more or less common origin from the trigonum fibrosum dextrum and lie in the atrial wall immediately under the endocardium and produce the ridges of the annulus fossæ ovalis, the torus Loweri, and the crista terminalis; they are intimately concerned in the determination of the form of the systolic atrium, as has already been described (p. 65). Four such bundles may be recognised: (*a*) The fasciculus terminalis (tænia terminalis, Keith) begins on the septum just above the atrio-ventricular orifice and runs upwards on it as rather a flat band as far as the orifice of the superior vena cava (fig. 43). As a more rounded bundle it then runs laterally over the roof of the atrium, passing anterior to the caval opening, and is continued into the crista terminalis of which it forms the substance. Its fibres are continued from its lateral edge as the musculi pectinati, while below they end partly in the Eustachian valve and partly on the posterior wall of the orifice of the inferior vena cava. (*b*) The fasciculus limbicus superior is an arched bundle which forms the substance of the upper and posterior limbs of the limbus fossæ ovalis. At the uppermost part of the limbus it divides into two parts, the lower of which (superior limbic band) continues to encircle the fossa ovalis and ends below on the posterior and lateral walls of the orifice of the inferior vena cava; the upper division runs laterally on the septum and as (*c*) the fasciculus Loweri (Keith) forms the substance of the torus Loweri; its fibres end in the crista terminalis. (*d*) The fasciculus limbicus inferior (the inferior limbic band, Keith) forms the anterior part of the limbus fossæ ovalis and then extends on to the medial and anterior walls of the orifice of the inferior vena cava; a few of its fibres end in the medial part of the Eustachian valve. There are no such definite bands to be displayed on the interior of the left atrium, apart perhaps from that described by Keith as the tænia terminalis sinistra (p. 66). It takes origin in the trigonum fibrosum dextrum, runs transversely across the roof between the atrial appendage and the upper pulmonary veins, along which line a groove appears on the surface of the systolic atrium (p. 65); and it terminates, in part, in the left side of the left annulus fibrosus. It is in no manner to be compared in its size with the crista terminalis of the right atrium.

The Ventricular Musculature. The muscular bundles of the ventricles are arranged in more intricate combinations than the bundles of the atria. It has been suggested that the difference in the arrangement is produced by the torsion of the ventricular loop, the ventricular fibres being laid down in spirals on spirally twisted surfaces; the atria undergo no twisting and the atrial fibres, therefore, are simple annular bands (Walmsley). In an introductory account such as this is, it is not possible to refer to all the descriptions of the ventricular muscle that have been made; a full account of the literature of the subject is given by Tandler, and analyses of it have been made by MacCallum and Mall. The architecture of the ventricles in other vertebrates than mammals is described by Owen, Pettigrew, and Shaner.

It is most convenient first to give a short description, on a purely topographical basis, of the layers which can be defined.

The fibres on the surface of the ventricle, **superficial fibres** (vortex fibres, Tandler; superficial bulbo-spiral and sino-spiral systems, Mall), arise from the tendinous structures round the orifices at the base of the heart and appear from the whole circumference of the coronary sulcus (figs. 47 and 48). They

extend, in a spiral course, the fibres over the right ventricle more transversely and those over the left ventricle more vertically, towards the apex of the heart where, with an abrupt twist which forms the vortex, they pass into the interior of the left ventricle and are continued there, as ascending fibres, into the papillary muscles and as the innermost muscular layer of that cavity. They may be arranged in two groups, the anterior and the posterior superficial fibres.

That the superficial fibres turn in at the apex of the heart and spread out on the inside of the left ventricle was known to, and described by, LOWER (Tractus de corde, 1669), though it is stated by HALLER and is implied by MALL that it had previously been described by BORELLI; and it forms part of all the descriptions of the ventricular muscle which have since been given. There were thus early recognised outer and inner muscular layers, the fibres of which are continuous at the apex of the left ventricle. It has been thought that a similar continuity is to be found at the base of the heart, and that few if any of the bundles are attached to the tendinous rings. But though some bundles of the deep layer may turn at the atrio-ventricular openings, the ends of all the fasciculi are attached to the fibrous structures at the base either directly or through the medium of the chordæ tendineæ and the cusps of the valves.

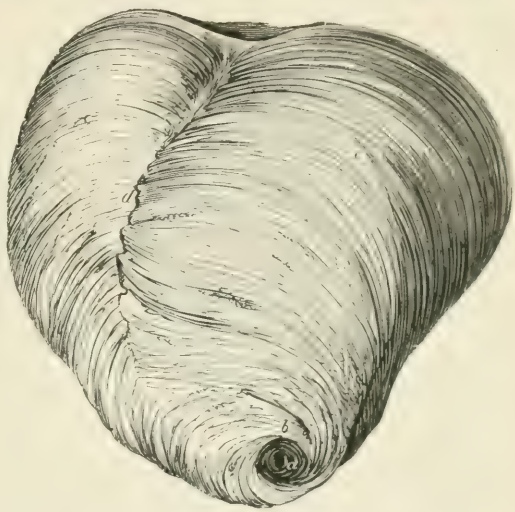


FIG. 49.—SURFACE FIBRES OF THE VENTRICLES OF THE HUMAN HEART FROM THE FRONT AND BELOW. (REID.)

The **anterior superficial fibres** (superficial bulbo-spiral fibres, MALL) arise from the anterior parts of the left and right annuli fibrosi and from the conus tendon, and descend obliquely downwards and to the left as a broad sheet over the anterior surface of the heart. Near the apex of the heart they become gathered together in a more compact bundle, groups of fibres being superimposed on other groups; and having reached the posterior surface of the left ventricle they turn into the vortex as the posterior vortex horn (see p. 75) and disappear (fig. 47). Many of the fibres of this sheet, however, dip in at the anterior interventricular groove and make it difficult to raise it from the underlying layers without free division of the penetrating bundles.

The **posterior superficial fibres** (superficial sino-spiral fibres, MALL) arise from the posterior parts of the left and right annuli fibrosi, and as a well-defined though thin layer descend obliquely downwards and to the right, on the whole more vertically than the anterior fibres, towards the apex of the heart (fig. 48). Turning round the margo acutus near the apex of the heart the fibres become gathered together and turn into the vortex as the anterior vortex horn. This sheet is more easily defined and separated from the surface than the anterior sheet for it differs more in the direction of its fibres from those immediately beneath it.

These superficial fibres form a complete covering for the heart, thinner above than below, but at many places, especially at the margo acutus and on the anterior surface of the right ventricle, connections with the deeper layers may be demonstrated, slips of fibres emerging to the surface (and often bridging over branches

of the coronary arteries) and other slips passing from the surface into the heart substance. If these bundles are broken through, the superficial layer can be separated from the underlying layers. At the vortex the superficial fibres form the whole thickness of the heart wall; and having turned in at the vortex they ascend on the inner surface of the left ventricle in the trabeculæ and papillary muscles and on the surface of the septum, and finally are attached again to the fibrous rings from which they arise. In general, a bundle which lies superficial on one wall ascends as a deep bundle on the opposite wall; thus fibres which descend on the surface in front ascend on the inner surface of the posterior wall.

The superficial fibres thus complete a figure of 8 loop which, however, is open above where the ends are attached to the fibrous rings at the base. The one limb of the loop lies on the outer surface of the ventricle and the other on its inner surface, and, as was pointed out by WEBER, the two limbs radiate spirally from the apex to the base in opposite directions, so that if the heart be viewed as an object the fibres run downwards from left to right on the outer surface and from right to left on the inner surface.

Among the superficial fibres a band is very frequently to be found issuing from the coronary sulcus and descending along the posterior interventricular groove to the apex of the heart; it appears to be better marked in the newborn than in the adult, that is, relatively it is better developed. It was figured by WOLFF and HENLE and was fully described by MALL, and it should probably be included in an ordinary description and not classed as a variation.

The **deep fibres** may be described in three groups: (1) Fibres belonging to the right ventricle; (2) fibres belonging to the left ventricle; and (3) interventricular fibres.

1. The fibres of the **right ventricle** (deep sino-spiral fibres, MALL) arise, under cover of the posterior superficial fibres, from the posterior circumference of the left and right annuli fibrosi and from the intervening parts of the trigonum dextrum, and run towards the right on the posterior wall of the right ventricle. The upper fibres are almost horizontal, and as they run forwards they closely encircle the right atrio-ventricular orifice [1]; the lower fibres are more oblique, but they are always more transverse than the overlying posterior superficial fibres. After a course of varying length downwards and forwards these deep fibres suddenly bend on themselves, turn upwards, and run towards the heart base. The more caudally placed fibres pass deep to the more cranial fibres, a peculiar interlocking arrangement thus resulting; and they spread out in the trabeculæ on the inner surface of the right ventricle and pass into the papillary muscles. The highest fibres pass most anteriorly and, having reached the anterior interventricular furrow, they dip into the septum and cover its right surface. On the anterior surface of the ventricle some fibres arise from the conus tendon and form, with some fibres from the anterior side of the right atrio-ventricular ring, a layer which encircles the conus.

2. The deep fibres of the **left ventricle** form the thickest layers of the heart musculature. They arise, under cover of the anterior superficial fibres, from the anterior parts of the left annulus fibrosus and trigonum fibrosum and from the left part of the right annulus, and run obliquely to the left and downwards on the front of the left ventricle. They lie more transversely than the superficial fibres and form several layers, the bundles of which are continuously changing their plane (see below). They pass round the margo obtusus on to the posterior surface of the heart, the lowest fibres not reaching the apex which is therefore entirely free of deep fibres; and they continue on the posterior wall until they reach the septum, into which they bend. From the septum some of the fibres are

[1] In the bird's heart these fibres form the muscular valve of the right atrio-ventricular orifice.

continued into the anterior papillary muscle, and through it to the aortic root, while the others are continued round the ventricular wall a second time and pass into the posterior papillary muscle, and running vertically upwards in it end in the right trigonum fibrosum. (It is this layer which was unrolled by MacCallum and Mall, as is stated in the discussion below.) At the base of the ventricle there are fibres which arise in front from the left trigonum and, encircling the atrio-ventricular orifice, pass round the margo obtusus to be attached to the right trigonum behind.

The deep fibres of the left ventricle vary considerably in their mass and arrangement in the adult heart, and it has been recorded that in the dilated heart with a thin wall they are barely visible and that in the hypertrophied heart they are excessively developed. They are relatively insignificant in number in the newborn and the young child; they must therefore increase and grow very markedly in childhood.

3. The **interventricular fibres** arise from the left annulus fibrosus and from the lower and posterior margin of the septum membranaceum, cross the septum, and run downwards on its right surface parallel to the long axis of the heart; there are small accessions to them from the septal papillary muscles. Near the apex of the heart they turn to the left and, mingling with the posterior superficial fibres in the anterior horn of the vortex, are inserted into the papillary muscles of the left ventricle. This bundle of fibres was fully described by MacCallum in the pig and by Mall and Knower in the human heart. It was first described by Senac (1774), and was described and figured almost accurately by Gerdy, and has been repeatedly identified since; Weber, however, denied the existence of the bundle.

Fig. 50.—View of the fibres of the sheep's heart, dissected at the apex to show the "vortex." (Pettigrew.)

a, *a*, fibres entering the apex posteriorly at *b*; *c*, *c*, fibres entering the apex anteriorly at *d*.

The peculiar spiral concentration of the fibres of the heart at the apex is known as the **vortex**. It is produced, as already described, by the twisting or interlocking of the superficial fibres as they pass to be continuous with those in the interior. It possesses two horns, an anterior and a posterior, which are easily separated from one another and are then seen to consist of the posterior and anterior superficial fibres gathered into compact masses.

As has already been stated, the arrangement of the **ventricular muscle fibres** has received great attention from anatomists; and mention has been made of the descriptions given by Vesalius, Borelli, and Lower. The account given by Lower is remarkably complete and formed the basis of the further work done at Paris under Winslow and later at Leipzig under Weber and Ludwig. The former school confined themselves to a detailed description of the layers into which the heart wall may be divided, and the course and attachments of the constituent fasciculi; while in the latter school a more functional interpretation was sought and the heart muscle was examined as a whole. Winslow himself (*Mem. de l'Acad. de Sc.*, 1711: "Exposition anatomique de la structure du corps humain," 1732) did not add much to the account given by Lower; his description of the ventricles, however, as "two (muscular) bags contained in a third" is often quoted. Gerdy ("Recherches . . . d'anatomie," Paris, 1823), a pupil of Winslow's school, followed Winslow's method of description and wrote a practically complete though complicated account of the arrangement of the muscular layers of the ventricles; his figures, however, are often criticised. Mall, in the main, has followed Gerdy's account and has recorded his appreciation of his work; and it is unlikely that there are now any great changes to be made in the pure description of the ventricular muscle. Ludwig ("Ueber den Bau und

d. Bewegungen der Herzventrikel" (*Zeitschr. f. rat. Med.*, 1849) made a detailed study of the course of the fibres at different parts and an analysis of their attachments, and showed that each piece of the ventricle which possesses the entire thickness of the wall, has a system of fibres on its outer surface and a system at approximately right angles to it on its inner surface, and between these a series of layers in a regular succession of transition of direction from the one to the other (fig. 51); but he believed that any separation of the heart wall into layers, with the exception of the superficial layer, must be considered to be artificial. LUDWIG also showed that tendinous

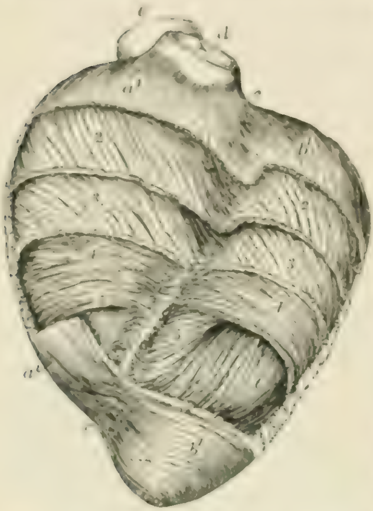


FIG. 51.—VIEW OF A PARTIAL DISSECTION OF THE FIBRES OF THE ANTERIOR WALL OF THE VENTRICLES IN A SHEEP'S HEART, DESIGNED TO SHOW THE DIFFERENT DEGREES OF OBLIQUITY OF THE FIBRES. (ALLEN THOMSON.)

At the base and apex the superficial fibres are displayed: in the intervening space, more and more of the fibres have been removed from above downwards, reaching to a greater depth on the left than on the right side. a^1, a^1, the superficial fibres of the right ventricle; b^1, b^1, the same of the left ventricle; at 2 these fibres have been removed so as to expose those underneath, which are seen to have the same direction as the superficial ones over the left ventricle, but different over the right; at 3 some of these have been removed, but the direction is only slightly different; 4, transverse or annular fibres occupying the middle of the thickness of the ventricular walls; 6, 7, internal fibres passing downwards towards the apex to emerge at the whorl; between c, c, the anterior coronary or interventricular groove, over which the superficial fibres are seen crossing; in the remaining part of the groove, some of the deeper fibres turn backwards into the septum; d, the pulmonary artery; e, the aorta.

parts not being present in the myocardium proper, the muscle fibres can be attached only to the outer and inner circumferences of the rings at the base and at the apices of the papillary muscles; and he described the origin, course, and termination of a series of bands of fibres on the outer and inner surfaces of the heart, showed that they are continuous with one another at the apex of the left ventricle, and that they followed the figure-of-8 course previously described by GERDY. He also clearly described, as WINSLOW had done, that as the outer and inner sheets are followed upwards from the apex to the base more and more layers are interposed between them. PETTIGREW (*Proc. Roy. Soc. Ed.*, 1866; *Phil. Trans. Roy. Soc.*, 104, 1864), whose account was largely followed in the last edition of this work, but who does not seem to have known of Ludwig's descriptions, arranged the musculature in layers according to differences in their direction. He described seven layers (fig. 51), three outer, three inner, and one central, and stated that the first and seventh, second and sixth, and third and fifth, are continuous at the apex of the left ventricle and along the anterior interventricular groove. He gave a good description of the vortex. This method of description, the artificial subdivision of the musculature into layers and the description of each layer, was continued by WINKLER ("Beitrage z. Kentniss d. Herzmuskulatur," *Arch. f. Anat.*, 1865; "Schichten u. Teilung d. primitiven Muskelbündel im Herzen," *ibid.*, 1867) and by KREHL ("Ueber d. Bedeutung d. Herzmuskels," *Arb. a. d. med. Klinik zu Leipzig*, 1893), the latter described the conus tendon and gave a good account of the middle layer, which he wrongly described, however, as a cylindrical basket of circular fibres which had no terminal attachments and could be shelled out of the middle of the wall of the left ventricle. MACCALLUM ("Architecture and Growth of the Ventricles of the Heart," *Johns Hopkins Hospital Reports*, vol. ix., 1900), whose work was afterwards amplified by MALL (*Am. Jour. Anat.*, vol. xi., 1911), studied the musculature of fœtal (pig) hearts. He described superficial and deep layers much in the manner given above, but demonstrated that when the thin

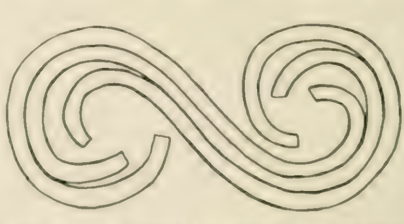


FIG. 52.—A DIAGRAM OF THE ARRANGEMENT OF THE DEEP MUSCULATURE OF THE VENTRICLES. (After MACCALLUM.)

superficial muscles are removed the deep musculature consists of a scroll shaped band wound round the walls of both ventricles (fig. 52); that it possesses tendons at each end; that it is continuous across the septum from the right to the left ventricle; and that as it grows older the septal part remains thin while the parts in the ventricular walls greatly increase in thickness but that still the ventricles can be unrolled and the continuity of the band displayed.

All future work, which must be interpretative rather than descriptive, should be based, like MacCallum's work, on the development of the muscle fibres; and as these are laid down in human embryos of 20 mm. length, and as the course of the fibres cannot be followed with certainty in serial sections, the difficulties are very great. The present position may be thus summarised. (1) The layers on the outside of the ventricle wall are at right angles to those on the inside and between these the direction gradually changes from the one to the other. The fibres shorten and thicken in contraction, the shortening being in the direction of the fibres, which varies, and the thickening being in the one direction which is common to them all, that is in the direction of the thickness of the heart wall; so that in systole the heart wall becomes thicker. (2) No simple scheme, which applies to all parts of the heart wall, can be given of the course of the muscle bundles, but in general the wall consists of V-shaped loops lying within

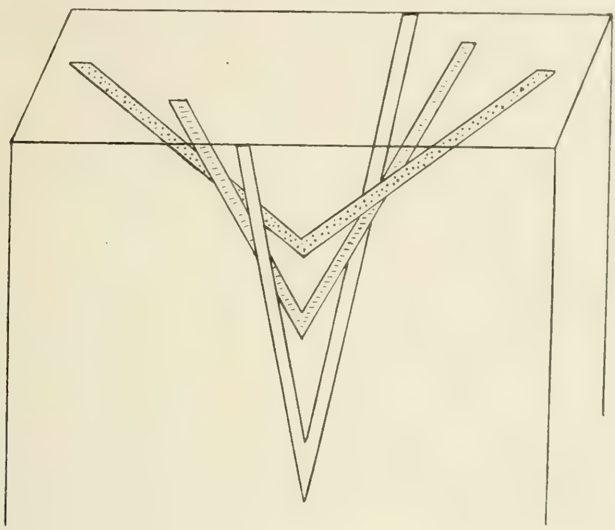


Fig. 53.—A diagram of the arrangement of the ventricular muscle fibres in loops. (After Mall.)

one another. The outer loops form acute angles at the heart apex with one limb on the superficial surface and the other on the deep surface; towards the middle of the wall the loops do not reach the apex, the fibres are less vertical in direction, and the angle is less acute; and in the middle of the wall the fibre is shorter, is nearly transverse in direction, and the angle is obtuse (fig. 53). There is thus a constant progressive change in the direction of the fibres from one surface to the other. This change is the expression of a change in the direction of contraction, or morphologically of a change in the plane of the major anastomoses between the fibres. This simple scheme is of course distorted since the loops are not completed in one plane but pass round the ventricular wall; but it expresses the view that the ends of all the loops are open and are fixed to the fibrous rings at the base.

Dissection of the Ventricular Musculature of the Human Heart (after MacCallum, Mall, and Knower).—A proportion of the hearts taken from dissecting-room subjects preserved with carbolic acid are suitable for dissection by this method, but more satisfactory results are obtained from fresh hearts. They should be boiled from half an hour to two hours in water acidulated with acetic acid; longer boiling softens too much the fibrous tissue at the base. The atria are to be removed. The epicardium, blood vessels, and superficial fat are then entirely removed—there will be some destruction of the superficial muscles in early attempts; the superficial fibres will be exposed. These fibres may be separated into anterior and posterior sheets most easily at the vortex, by inserting the handle of a knife between its two horns which they form; and from there they may be traced upwards over the surface of the heart to their

origin at its base. The posterior superficial layer is to be divided along the left side of the posterior interventricular furrow and raised from the underlying muscle. The septum may now be split by rolling the right ventricle forwards and away from the left ventricle until the upper part of the interventricular band is exposed; this is to be cut across below its origin. The septal blood vessels are now well seen, and the membranous septum will be split and the atrio-ventricular bundle seen in a striking manner in this part of its course. The right and left ventricles may now be further unrolled and the course of the deep fibres of each side exposed; and the process is to be continued until the ventricles are opened into from the septal side. The superficial fibres may then be shown to turn round the deep fibres at the apex of the heart; but the further dissection of them, and of the deep fibres on the inner surface of the heart wall and in the papillary muscles is difficult and the results are less constant, and before it is attempted reference should be made to the authorities cited above.

The Connecting Systems of the Heart. The connecting systems [1] of the heart are those parts which preserve the muscular continuity between the primitive chambers, which otherwise are separated from one another by fibrous-tissue structures. They are two in number, and connect the sinus and the atrium and the atrium and the ventricle respectively; that part of the bulbus which is included in the ventricle is clothed with ventricular muscle, so that there is no system between these parts. The **atrio-ventricular system** consists of a band of muscle fibres with distinctive characters which commences in the wall of the right atrium, perforates the fibrous tissue between the atria and the ventricles, and terminates in a widely spread network of fibres, the fibres of Purkinje, in the walls of the ventricles (fig. 51). It connects together the musculature of the atrium and that of the ventricles and, it is believed, conducts from the atrium to the ventricles the stimulus which causes the ventricles to contract in sequence and in rhythm with the atria; it is, in short, considered to be the conducting and co-ordinating mechanism of cardiac contraction.[2] The **sino-atrial system** consists of a mass of similarly distinctive muscle fibres which lies at the junction between the superior vena cava and the right atrium. It is usually considered to be the place of origin of the stimulus of contraction, and is often described as the initiatory mechanism of cardiac contraction and the "pace-maker" of the heart. These two systems, composed of a specific musculature which is (usually) easily distinguished from the general myocardium,[3] have not yet been definitely shown to be connected together by similar specific muscle fibres.

A muscular connection between the atrial and ventricular musculatures was fully described by GASKELL in 1883 in the heart of the tortoise. The connection in the mammalian heart, which is more limited and more difficult to demonstrate, was first described by KENT in 1893 in the heart of the newborn rat.[4] It was

[1] The term "connecting system," which has been adopted here, is based, of course, entirely on a morphological concept of these structures and in complete disregard of all functional interpretations.

[2] This is not the place in which the function of these connecting systems may be discussed, but reference may be made to the views of MACKENZIE who considered that the heart muscle contracts only in response to stimuli from them, that is, that they are, for the heart muscle, stimulus-producing structures; he proposed, therefore, that they should be named the **genetic system**. These systems are believed to be non-contracting, but CURRAN has described movements of the right limb in the ox; whether the bundle is contractile or is not, it may be noted here, is not to be determined by histological study alone (see further, ERLANGER, CADY).

[3] There are great differences in the amount of the distinction between the connecting musculature and the myocardium in different animals; in ungulates the distinction is very striking, in the dog it is slight. The meaning of these differences is unknown.

[4] The descriptions given by KENT include a right lateral muscular connection bridging over the coronary sulcus; it has not been confirmed as a normal structure by later work, though there is some evidence in clinical and experimental work that such a connection exists (LEWIS).

more fully described and was figured by HIS (junr.) in the same year in several animals, and has since been generally known as the atrio-ventricular bundle of HIS.[1] HIS described the band as having "its origin on the posterior wall of the right atrium near the atrial septum in the atrio-ventricular furrow," and correctly defined its course "anteriorly on the upper edge of the ventricular septum until near the aorta it divides into right and left limbs"; his description, however, of the termination of the left limb "in the base of the aortic cusp of the mitral valve" is incorrect.[2] In 1904 RETZER (in the sheep, pig, calf, horse, dog, and man) confirmed the major part of the descriptions of HIS and made the first diagram of a dissection of the bundle in man; and he recognised and described the fibrous sheath which surrounds the bundle and isolates it from the myocardium. About the same time BRAÜNIG also made a confirmatory study on an extensive series of mammals. The detailed and exhaustive work of TAWARA, conducted under ASCHOFF, on which all later researches are founded, appeared in 1906, and it was then established (in the pig, sheep, calf, cat, various rodents, and man) that the atrio-ventricular bundle begins in the atrio-ventricular node of Tawara in the lower part of the atrial septum, and that it terminates in the widely spread network of Purkinje fibres in the walls of the ventricles; and the continuity of these parts (the node, the bundle, and Purkinje fibres) being established, the whole system was defined as the initiatory and conducting system (*Reisleitungssystem*, ASCHOFF and TAWARA) of the cardiac contraction.[3] The atrio-ventricular system and its connections are best seen, among mammals, in the hearts of ungulates, and first studies of it should be made on the sheep or the ox.

In 1906 MACKENZIE and WENCKEBACH, working independently, postulated on clinical grounds the presence of a connecting mechanism between the sinus and the atrium, as would indeed be expected from the facts of comparative anatomy; and the latter pointed out as its structural basis a peculiar system of pale muscle fibres passing from the superior vena cava to the right atrium. This band, now usually known as the bundle of WENCKEBACH, was afterwards shown to belong to the atrial musculature and its fibres demonstrated to have the same structure as atrial fibres. At a later date KEITH and FLACK described at the junction of the superior cava and the right atrium the node now known as the sino-atrial node, the structure of which resembles that of the node of Tawara. The presence of the node has since been confirmed in a large series of mammals.

No distinctive path between the sino-atrial and atrio-ventricular nodes has yet been demonstrated, though MINE's work on the conduction of the impulse, as shown by electrical changes without form changes in the atrial muscle, suggests

---

TANDLER, however, describes one specimen in which he found a muscle band which arose from the right atrium, crossed the coronary sulcus embedded in fat near the posterior longitudinal sulcus, and ended in the ventricular muscle. TODD (in COWDRY, "Special Histology," vol. ii., 1928) has again emphasised the presence of multiple atrio-ventricular connections.

[1] It has been held that PALADINO described a specific atrio-ventricular connection in 1876 (see v. BARDELEBEN). A discussion of this claim is to be found in the works of RETZER, TANDLER, DE GAETANI, and PALADINO; it would appear that it has not been established.

[2] Such a termination of an aberrant left branch has been described in abnormal hearts (see MORISON, *Jour. Anat.*, vol. xlvii.); and frequently in normal hearts an abruptly ending process can be traced in this direction.

[3] It was stated by DE GAETANI (1911) that the atrio-ventricular bundle is an inconstant formation in man. In fifty human hearts, he says, he found the bundle (in macroscopic preparation) only in twenty-two; in twenty-eight hearts he was unable to demonstrate it. DOGIEL (1910) has expressed a similar opinion. A statement on this matter is made below.

that such a path exists. It is assumed, of course, that the atrial muscle would not conduct an impulse which could be recorded electrically without itself contracting. (See below for a further statement.)

The Atrio-Ventricular System.—This system may be divided, for descriptive purposes, into (*a*) the atrio-ventricular node of TAWARA, (*b*) the atrio-ventricular bundle of HIS, and (*c*) the fibres of PURKINJE. The node and the bundle can be demonstrated by dissection in most formalin fixed human hearts, but not with certainty in all; fresh hearts are not so useful. The fibres of Purkinje can be revealed only by the use of special methods and require microscopic examination to be studied.

(*a*) The **atrio-ventricular node**, or node of TAWARA, in man, is, when it is well developed, an oval formation about 6 mm. in length, 2 to 3 mm. in breadth, and 1 mm. thick. It lies in the wall of the right atrium within a triangle, the

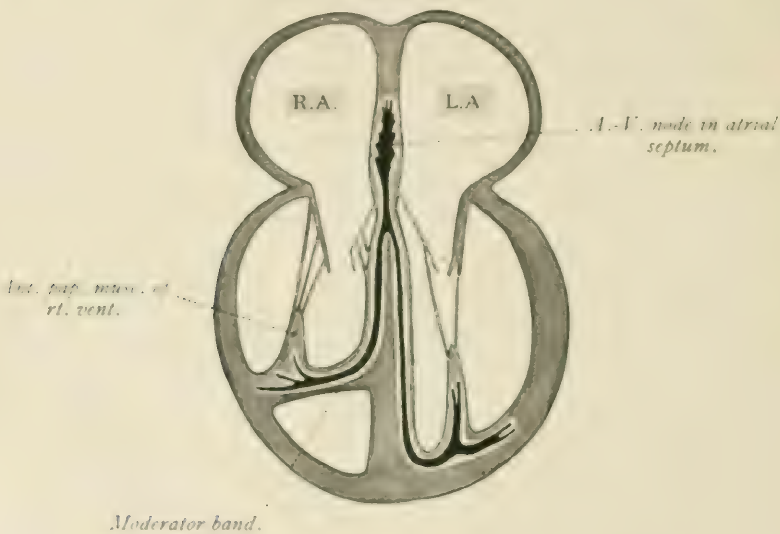


FIG. 54.—A DIAGRAM OF THE ATRIO-VENTRICULAR SYSTEM.

boundaries of which are thus defined by KOCH (fig. 55); the caudal boundary is formed by the attached edge of the septal cusp of the tricuspid valve, the cranial boundary by the tendon of Todaro (see p. 33), and the posterior boundary by the orifice of the coronary sinus. In the field thus defined the node lies nearer the apical angle, that is in the angle between the tendon of Todaro and the cusp attachment, and parallel to the attached edge of the cusp. The node, in this position, lies immediately under the right (or posterior, see p. 48) cusp of the aortic valve, a relationship which was over emphasised in the early descriptions. It is covered superficially by a thin layer ($\frac{1}{2}$ to 1 mm. thick) of vertical atrial muscle fibres, while deep to it there is the posterior part of the trigonum fibrosum dextrum. In the fresh heart the node can be distinguished from the surrounding structures by its lighter, almost yellowish, colour. The ventricular end of the node gradually passes into the atrio-ventricular bundle, there being no obvious boundary between the two. The atrial boundary is indefinite to the naked eye, the node appearing to pass gradually into the atrial muscle in a number of prolongations, one of which, running laterally under the mouth of the coronary sinus, is much larger than the others.

The oval form of the node is sometimes not very obvious, and the atrio-ventricular bundle may then appear to begin as a beaded band, as indeed the node was figured by KEITH and FLACK; it certainly varies considerably in its size. It is much better developed and apparently more constant in its form and size in the hearts of the larger ungulates, but in the sheep heart it is not to be defined from the bundle by the naked eye.

There has been, and there is, it should be stated, a considerable amount of support for the view that the node and the field of the right atrium in which it lies are derivatives of the sinus; and, further, that the node represents a left sinus derivative and that the sino-atrial node is the corresponding right sinus derivative (see p. 96). KOCH seems to have been the first to express this view, and he has been supported in it, in whole or in part, by RETZER, DE WITT, and I. MACKENZIE; RETZER, indeed, has named the bundle the sino-ventricular bundle, believing that it passes from the sinus to the ventricle. On strictly embryological grounds this view, so far as it relates to the atrial wall, cannot be confirmed, as has already been stated in the account of the development of these parts (p. 41); but for a further discussion see the "Comparative Anatomy of the Connecting System."

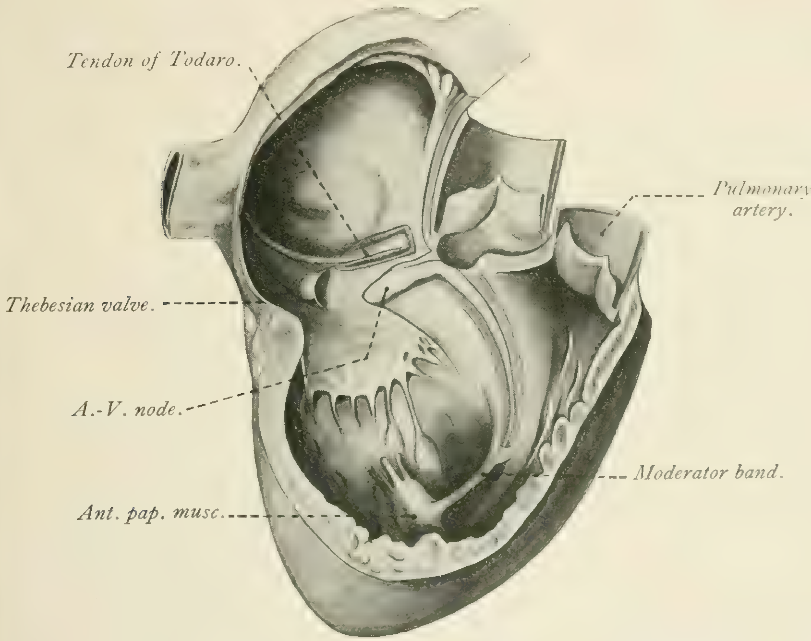


FIG. 55.—DISSECTION OF THE ATRIO-VENTRICULAR NODE AND THE RIGHT LIMB OF THE ATRIO-VENTRICULAR BUNDLE.

The septal cusp of the tricuspid valve is partly cut away, and above it the main stem of the bundle is seen at the lower margin of the septum membranaceum.

(*b*) The **atrio-ventricular bundle**, or bundle of HIS (fig. 54), consists of a short stem, the crus commune, which passes from the node into the ventricular septum and there divides into right and left limbs for the right and left ventricles.

The **stem** of the bundle (fig. 55) arises from the ventricular end of the atrio-ventricular node, and passes almost at once into the posterior part of the trigonum fibrosum dextrum (fig. 46), in the substance of which it lies surrounded by its own sheath (see below). It runs anteriorly in the trigone to the posterior end of the attachment of the septum membranaceum (fig. 45 and p. 68), and gains there a position on the summit of the muscular part of the ventricular septum. Riding on the muscular septum, it continues its course along the posterior circumference of the membranous septum and opposite its inferior circumference divides into two limbs. The length of the stem is generally about 1 cm. (11 mm., DE WITT,

4 to 11 mm., DE GAETANI), but is difficult to determine owing to the want of demarcation between it and the node. It is variable in its form, in some hearts being a flattened band and in others a rounded cord; its breadth and thickness, therefore, are variable, and it may be from 1·5 to 4 mm. broad and from ·5 to 1·5 mm. thick.

The stem of the bundle was the first part described by HIS, but it is of interest to note that it is accurately figured at its place of division, without being named or its significance recognised, by HENLE in fig. 23, "Handbuch der Gefässlehre" (1876). It was first figured macroscopically by RETZER, and has since been figured by HOLL, KEITH, CURRAN, TANDLER, DE GAETANI, DE WITT—who has modelled it—VERMES, and others. It should be noted in these figures that it does not lie exactly on the summit of the septum carneum, but definitely a little on the right side; so that it is covered by a thinner layer on the right than on the left side. The best view of the division of the stem into its two limbs is obtained if the atria be removed and the aorta and the atrio-ventricular cusps dissected away until the septum membranaceum is well exposed; this septum is then cut away and the bundle is exposed from above. The stem may pass round the right edge of the trigonum instead of piercing it, in which case it pierces the place of insertion of the septal cusp of the tricuspid valve. In the ungulate heart it lies in a groove on the right surface of the os cordis.

The **right limb** lies in the same sagittal plane as the stem and is the more direct continuation of it. It descends, more or less close to the surface, on the right side of the ventricular septum and, as a rounded or triangular bundle 1 to 2 mm. thick, or sometimes as a flattened band, it may be followed to the septal origin of the trabecula septo-marginalis (moderator band). It then enters this band and crosses the cavity of the ventricle in it, and may usually be traced to the base of the anterior papillary muscle (fig. 55), where it passes into its terminal branches.

In macroscopic preparations there are great individual differences in the distal end of the right limb, that is in the manner and position of its passage into its terminal ramification; but as stated above it can usually be followed in the moderator band to the base of the anterior papillary muscle. But it must also be stated, as has already been done by DE GAETANI and DOGIEL, that in some hearts the right limb of the bundle cannot be displayed in the septum; and that sometimes even microscopic examination fails to reveal any tract of specific muscle with a sheath in the usual position. It must be concluded, therefore, that in some instances the right limb assumes the characters of the normal myocardium soon after it has left the main stem (see fuller, KEITH and CURRAN), or that there is a very early scattering of the fibres which are normally grouped together to form the limb. Its course from its origin to the moderator band is as follows. It runs at first along the lower circumference of the septum membranaceum, continuing the course of the stem, and is covered here by some of the muscle fibres inserted into the septum. It then turns downwards into the muscular septum, and, as it turns, it lies immediately beneath the endocardium in the lower anterior boundary between the membranous septum and the muscle; the length of the subendocardial part is variable, but the recognition of its position is important for it is the most suitable part of the limb to expose first in a macroscopic demonstration. More or less deeply embedded in the septum, the right limb now runs to the base of the medial papillary muscle of the septum. This muscle, as already stated (p. 54), is variable in its size and sometimes is so slightly developed that the chordæ tendineæ arise directly from a tendinous expansion; the bundle lies directly under this area. If the papillary muscle is well developed the bundle gives off a branch which runs into it (UNGAR). From this position the right limb runs to the origin of the moderator band, more or less along the boundary between the "inflowing" and "outflowing" parts of the ventricle; it gradually becomes more superficial and its lower part can usually be seen through the endocardium. In the moderator band it lies on the surface. In some animals (e.g., the tapir, TANDLER) the moderator band consists solely of the end of the right limb; this condition is sometimes closely approximated in man (WALMSLEY).

The **left limb** is a broad thin band. Its fibres arise in successive groups from the main stem and pass to the left from it at acute angles; and they form a relatively loose structure in which, not infrequently, there are longitudinal clefts. The band appears in the "outflowing" part of the left ventricle, at

the upper border of the septum carneum and just below the anterior part of the attached margin of the right cusp of the aortic valve (fig. 56); there is very little variation in this position of emergence. It lies immediately below the endocardium, through which it can be seen; but it is so thin (being only a fraction of a millimetre in thickness) that it is difficult to raise from its bed and to define from the neighbouring parts. It runs downwards, and slightly forwards, towards the apex of the ventricle, and after a shorter or longer course, but usually in the middle third of the septum, it divides into two branches of about equal size. The anterior branch turns sharply forwards across the smooth "outflowing" part of the septum, and reaching the trabeculæ on the medial side of the anterior papillary muscle, it passes in these trabeculæ to the base of this muscle. The posterior branch continues downwards in the line of the main limb (fig. 56) and, in the trabeculæ on the medial side of its base, reaches the posterior papillary muscle.

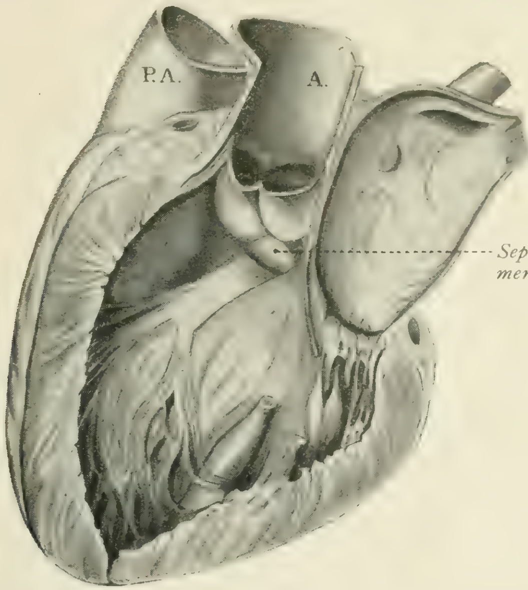


FIG. 56.—DISSECTION TO SHOW THE LEFT LIMB OF THE ATRIO-VENTRICULAR BUNDLE. A., aorta; P.A., pulmonary artery.

It has been frequently pointed out (MÖNCKEBERG, NAGAYO, HOLL), and has already been mentioned (p. 27), that opaque interlacing streaks are to be seen in the endocardium at many parts of the left ventricle, especially in its "outflowing" part where there is a considerable amount of smooth endocardial muscle (see p. 27). These streaks are liable to be mistaken for ramifications of the left limb, but as they are endocardial structures, and are removed with it, they can be distinguished by careful examination and a knowledge of their structure. The branches of the bundle are most easily detected in the lower third of the septum; in the upper third some experience is needed accurately to define the parent limb. In the region of the trabeculæ to which they pass, the branches divide into separate anastomosing bundles. Some of these bundles, forming the so-called "false tendons," pass across the cavity of the ventricle to the base of the papillary muscles; in some animals (the tapir, TANDLER) the two branches of the limb behave in this way, that is, they run as free bands through the cavity of the ventricle. The false tendons are described on p. 47.

The place of division of the posterior limb is, as is stated above, subject to variation; sometimes it is so high on the septum that there is only a very short main limb. Sometimes the limb divides into three branches, the third branch being a middle one between the anterior and posterior branches.

Histology of the Atrio-Ventricular System.—The atrio-ventricular node and bundle are readily distinguished from the surrounding myocardium in almost all modes of staining by their lighter colour, that is, their muscle fibres are stained less intensely with the myosin stain;

FIG. 57A.—THE RIGHT LIMB OF THE ATRIO-VENTRICULAR BUNDLE OF THE HUMAN HEART.
(Microphotograph.)

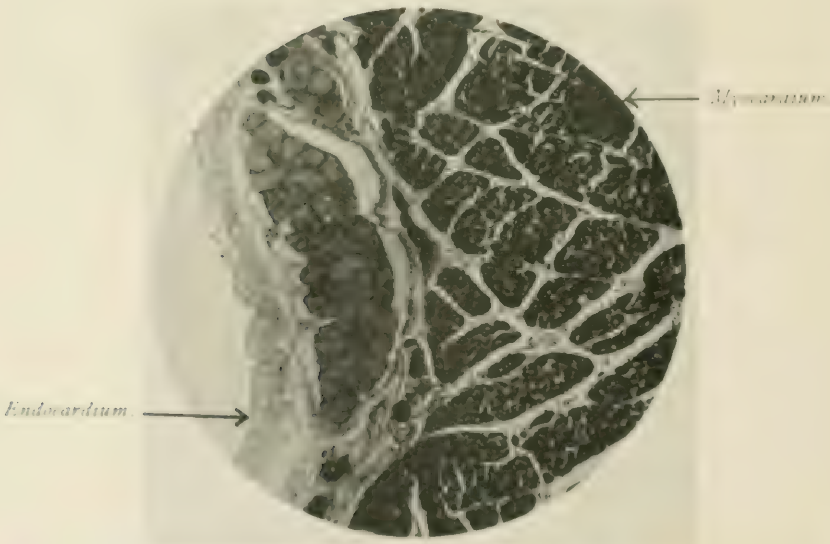


FIG. 57B.—A BUNDLE OF PURKINJE FIBRES FROM THE RIGHT VENTRICLE OF THE SHEEP.
(Microphotograph.)
The large size of the fibres and the sheath round the bundle are well shown.

and in Van Gieson preparations it is also shown that these parts are separated from the other musculature by a thick layer of fibrous tissue which forms a distinct sheath for the bundle and its branches, but surrounds and pervades the node as a reticulum.

The arrangement of the muscle fibres at the node was succinctly described by TAWARA as an entanglement; the separate bundles are richly commingled and change their course so

frequently that it is impossible to obtain more than a short length of them in sections. The fibres are smaller than those of the myocardium. They are rich in protoplasm; the nuclei, relatively large in number and oval in shape as a rule and thus differing from the rod-like nuclei of the myocardial fibres, lie in the centre of the fibres, though border nuclei may be seen; longitudinal striation is distinct but sparse, the fibrils being small in number and confined in position to the peripheral parts of the fibres; and transverse striation is at the best necessarily insignificant. The contour of the fibres is irregular, that is, they increase and diminish in their transverse diameter. Cell boundaries, as distinct from the cement lines (*Kittlinien*) of the myocardial fibres, have been described by TAWARA and MÖNCKEBERG, but DE WITT describes the formation to be a syncytial one, several fibres fusing in star-like formations. In the sheep direct continuity is readily shown between the fibres of the node and those of the bundle; from the atrial end of the node a similar continuity with the atrial fibres cannot be certainly established, the appearances being a gradual fading of the nodal tissue into, and a replacement of it by, the usual atrial fibre formation (see CURRAN). The muscle fibres are embedded in the fibrous basis, in which also there are numerous nerve fibres (p. 87). There is a good blood supply to the node.

In the stem and the limbs of the **bundle** the fibres are more parallel, and form groups surrounded and separated from one another by fibrous-tissue sheaths (see below). In the ungulate heart the fibres are very much larger than the fibres of the myocardium; they are ten to twenty times longer, and in cross section the area may be fifty times greater (fig. 57). In the human heart they are smaller or very little larger than the myocardial fibres; and observations in other forms (cat, dog, mouse, guinea-pig) confirm the wide variation there is in the size of these fibres. In all forms, however, the fibres are of the same category, and have a structure essentially similar to that described above for those of the node; this similarity has led TODD to the conclusion that no special nodal tissue exists. It may be established in the sheep that the fibres branch and anastomose like those of the myocardium. Towards the termination of the limbs the fibres are more like those of the ventricular muscle and in man are more difficult to distinguish. Nerve fibres accompany the muscle fibres (see p. 87).

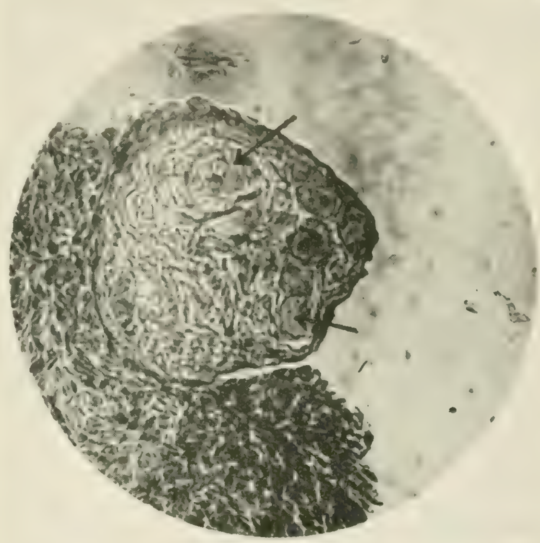


FIG. 58.—A BUNDLE OF PURKINJE FIBRES FROM THE RIGHT VENTRICLE OF THE HEN. (Microphotograph.)

(*c*) The **Purkinje fibres** are large muscle fibres of the same distinctive kind as those of the bundle which lie under the endocardium, in a network formation, over most parts of the walls of the ventricles, and also, at places, penetrate the wall for half its thickness; they have not been found in the outer part of the wall nor under the epicardium.[1] They may be grouped together in bundles or may be found singly. They are now recognised to be the terminal ramifications of the limbs of the atrio-ventricular bundle, though the limbs themselves have not yet been followed to all the parts where they exist; and they are considered, therefore, to be part of the connecting mechanism. The fibres are much larger, more numerous, and more distinctive in some forms than in others, and are best studied in the sheep and the ox; in man they are less different from the

[1] It has been suggested that they are to be found under the epicardium in the rabbit.

myocardial fibres. (For an account of the technique of preparation and details of structure, see Todd in "Special Histology," Cowdry, 1928.)

The Purkinje fibres were first described by Purkinje in 1845 in the sheep as "a network of grey gelatinous fibres," and have since been well recognised structures of the heart; but there have been very many interpretations of their nature and significance. In microscopical examination they are readily distinguished from ventricular muscle by their larger size and lighter colour in stained sections (fig. 59). A transverse section of a bundle of them appears, under low magnification, as a honeycomb formation, in the meshes of which are the large circular nuclei surrounded by a specially light zone. Under high magnification the fibres are seen to be rich in protoplasm; to possess very fine longitudinal fibrils, which are confined, however, to the peripheral parts and to be quite absent from the middle parts of the cell though (in the sheep) they may pass obliquely through it; and to have a large deeply staining oval nucleus in the central position surrounded by a clearer zone. Transverse striation is indistinct. There are appearances of cell boundaries, but a much more definite feature is that of irregular constrictions of the fibres along their length; and, as a rule, between each two constrictions a nucleus is to be found. The fibres anastomose with one another at their ends. Different kinds of fibres have been described, the extreme types being rod like and sheet-like forms. (See Tuffs, *Anat. Record*, vol. xxii.; Johnstone, *ibid.*, vol. xxiv.; Van der Stricht and Todd, *Johns Hopkins Hosp. Reports*, vol. xix.)

Purkinje fibres are present in the heart of the young animal and child in much the same form and size as in the adult. The view, which was widely held until the works of Tawara and Aschoff appeared, that they represent immature myocardial fibres or fibres arrested in development, has not been discussed. They are of the same category as those of the node and the bundle.

The Sheath of the Atrio-Ventricular Bundle. In its whole length the atrio-ventricular bundle (the common stem and the right and left limbs) is surrounded by a fibrous-tissue sheath of considerable thickness which separates it and isolates it from the myocardium; and this sheath is continued as a delicate investment round the Purkinje fibres up to their transition into the cardiac muscle fibres.[1] It is very plainly seen in sections stained with Van Gieson stain, which demonstrates it to be a thick covering of the bundle as a whole and finer investments of groups of its fibres. Curran has stated that the sheath is really the wall of a mucous bursa, containing a fluid similar to lymph but more viscid; the result being that on contraction of the surrounding myocardium the non-contractile bundle will be protected from pressure. This, however, has been contradicted by Lhamon and is not supported by Tandler; yet, in the sheep, a space is often to be seen between the fibres and the sheath, and in places a lining of very flat cells can be defined (Holmes), but such a space is not to be seen in the human heart. The presence of the sheath round it allows the bundle to be followed through the trigonum fibrosum dextrum, and permits injections of it to be made (p. 88).

Vessels of the Atrio-Ventricular System. The atrio-ventricular system is not so well supplied with blood vessels as the cardiac muscle (Johnstone, *Anat. Record*, vol. xxiv.), yet it is accompanied by several relatively large arteries which are definite branches of the coronary trunk within whose area of distribution (p. 102) the system in its course is placed. These branches, according to Haas, show relatively little variation, but the most recent work (Vischia, Fahr, Campbell) tends to emphasise a variability of the supply of the main stem and the upper parts of the limbs. The greater part of the bundle lies in the territory of the right coronary artery (p. 102) and is supplied by the following branches from it (Haas): (1) A branch, r. septi fibrosi, which runs forwards from the back of the heart between the atria and, after piercing the back part of the trigonum fibrosum dextrum, passes along the upper edge of the ventricular septum; it gives branches to the node and to the main stem as far as its division. (2) A branch, r. septi ventriculorum superior, which ramifies in the upper

[1] It has been specially investigated by Tawara, His, Mönckeberg, Keith, Holl, Fahr, Curran, and Lhamon in a large series of lower mammals and in man.

posterior part of the septum and supplies the posterior branch of the left limb. The anterior branch of the left limb lies in the territory of the left coronary artery and is supplied by it. The right limb lies in that part of the septum which is supplied by both coronary arteries; it receives, therefore, branches from in front and behind. One branch is to be found, often by naked eye dissection, passing from the septum with the right limb in the moderator band; it is usually a branch of the left coronary artery. (For a full description of it, see MOUCHET.)

Nerves of the Atrio-Ventricular System.—The nerves of the atrio-ventricular system have been studied chiefly in the hearts of ungulate animals, for in the ruminants, and especially in the calf, they are extremely numerous and large. The methylene-blue method is that by which the most satisfactory results are obtained, and, therefore, fresh material is necessary. ENGEL, WILSON, and DE WITT have described the presence of rich leashes of non-medullated fibres (and ENGEL also of medullated fibres) and numerous ganglion cells in the ruminants. The fibres come partly from the node and partly from ganglia on the posterior surface of the heart; they lose their medullary sheath and "join a complicated network of fine varicose fibres lying round individual cells and groups of cells" (WILSON). They may be followed to the terminal ramifications of the bundle and to the Purkinje system, but no definite end-organs have yet been described. The innervation of the node has been specially studied by MORISON and MEIKLEJOHN; nerves enter it from the ganglia lying on the back of the heart through the interatrial septum and break into small branches and these into single fibrils which ramify round the muscle cells. ENGEL, OPPENHEIMER, MEIKLEJOHN, and MORISON have described a non-medullated fibre system in the main stem and left limb of the bundle in the human heart, which is, however, much finer and more difficult to demonstrate than in the ungulate; but, according to MORISON, "enough was found to justify the belief that the elements of these parts were innervated, though the innervation was rather of the type of vasomotor innervation." The amount of innervation of the node and bundle which can be demonstrated varies in different animals.

Exposure of the Atrio-Ventricular Bundle.—The commencement of the right limb of the bundle is the part most easily exposed; this may be done by the following dissection. The septal cusp of the tricuspid valve is to be removed, and any chordæ tendineæ of the third order (p. 46) which may be present are to be cut away. The right surface of the septum membranaceum is thus exposed, and it will be seen that the posterior circumference of this septum is bounded by a flattened arched band of muscle open upwards and forwards. The endocardium is to be removed over this area so that the borders of the septum and the musculature are defined, and there will be exposed the short sub-endocardial part of the right limb lying on the muscle and in both directions passing under cover of its superficial fibres (p. 82). The limb may now be followed proximally to the main stem, and this to the trigonum fibrosum dextrum by cutting through the covering muscle. The substance of the trigonum is then cautiously split along the bundle until the insertion of the vertical atrial musculature into it is exposed; and, if this is carefully removed, the atrio-ventricular node will be displayed. The distal part of the right limb is relatively easy to follow along the septum; only under the macula tendinea septi (p. 51) is any difficulty likely to be experienced. The division of the main stem can be demonstrated by removing the septum membranaceum, the anterior part of the atrial septum, and a part of the aorta; and in this way the commencement of the left limb may be defined. The left limb may also be sought, as it appears in the left ventricle, in the angle between the anterior part of the attached border of the

right (posterior) cusp (p. 48) of the aortic valve and the upper edge of the septum carneum, by carefully separating the endocardium; further down very careful preparation is required as strong traction will separate the band with the endocardium.

The bundle and its ramifications can be very satisfactorily displayed in the ox, sheep, and horse by injecting its sheath with Indian ink; the ink remains within the sheath and is distributed along the branches of the bundle even to their terminal network ramification. The technique is fully described by AAGAARD and HALL, KING, and LHAMON. It has not yet been found possible satisfactorily to inject in this way the systems in man and the dog.

The attempt has also been made to demonstrate the terminal network by injecting the heart with, or immersing it in, such substances as will combine with the high glycogen content of these parts in the fresh heart and differentiate them from the surrounding musculature. The most successful results have been obtained by the use of iodine. The hearts are obtained as fresh as possible and, the atria and the ventricles having been opened, they are immersed in Lugol's solution; in about ten minutes the Purkinje system appears as dark brown lines (UNGAR). The colour deepens for two or three hours, but begins to fade in eight or ten days and gradually disappears. By this method the fibres have been demonstrated in the ox, sheep, and horse, but so far it has not been successfully employed in the human heart; this may be on account of the difficulty there is in obtaining the heart in a fresh enough condition, but it is also to be remembered that the glycogen content is smaller in man [1] than in the ungulates. The method, however, has been successful in the dog, in which the glycogen content of the fibres is believed closely to approach that of man. (The glycogen content of the different parts of the system has been studied in several forms by NAGAYO (working under ASCHOFF), MÖNCKEBERG, and others.)

The Sino-Atrial System.—The sino-atrial system, which is usually known as the sinus node or the node of KEITH and FLACK (*Ger.*, node of KOCH), lies in front of the lateral part of the superior vena cava in the upper part of the sulcus terminalis of the right atrium, that is, in the boundary between the sinus and atrial parts of that chamber.[2] It is placed comparatively superficially, being covered only by the epicardium and the subepicardial fat (fig. 59); there is usually a small definite mass of fat in this position. The sinus node has the form of a spindle, the upper part of which is enlarged; it has an average length of 2 cms., its greatest breadth is about 3 mm., and its thickness about 1 mm. It gives off from all along its length fine processes which, however, cannot be followed by dissection for any distance into the surrounding muscle; the processes from the upper part extend on to the anterior and lateral walls of the superior cava and mingle there with the spiral musculature round its termination. The narrow lower end of the node passes under a muscle band of varying size which springs from the posterior wall of the superior cava. This band, usually known as the bundle of WENCKEBACH,[3] bridges over the sulcus terminalis and joins the muscle bands of the musculi pectinati; histologically it has the structure of atrial muscle. The node is usually easily distinguished from the atrial musculature by its lighter colour and its greater density, due to the larger amount

[1] The glycogen content in man is apparently variable, and is diminished in atrophic and cachectic conditions.

[2] That the node lies on the sinus side of the boundary, as determined by the position of the venous valves, was demonstrated by OPPENHEIMER.

[3] It was this band which was described by WENCKEBACH as the specific sino-atrial connecting muscle (see p. 79).

of fibrous tissue it contains. The node can thus be more or less isolated from the surrounding tissue. A small artery will be found in its substance, giving branches to it, along its whole length.

Histology of the Sino-Atrial Node.—The node described by KEITH and FLACK has since been studied by KOCH, THOREL, OPPENHEIMER, UNGAR, BURIAN, and others, and though there are differences in the details, especially in the descriptions of the comparative microscopic anatomy of the node, the main facts of the original description are now well established. The discoverers of the node described it as a network of fibres, the ultimate structure of which it is difficult to determine on account of their free interlacement, only short lengths of the individual fibres being seen in sections, that is, the fibres do not form groups of uniform direction (fig. 60). The fibres in general are smaller in diameter than the atrial muscle fibres. They are yellow in sections stained by Van Gieson stain, and are then seen to be embedded in a thick interlacing fibrous tissue of relatively greater amount than in the atrio-ventricular node; and the two

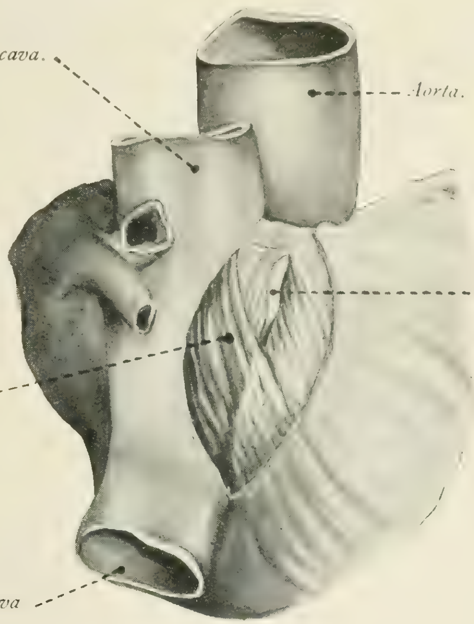


FIG. 59.—A DISSECTION EXPOSING THE SINO-ATRIAL NODE.

elements, muscle fibres and fibrous tissue, are arranged round the large artery which passes through the substance of the node. Transverse striation of the muscle fibres has not yet been certainly demonstrated, though BURIAN has figured and described such in the human heart, but fine longitudinal striation of the peripheral parts can generally be seen; the central parts of the fibres are much lighter in colour than the peripheral parts and contain the nuclei which are oval or round. Direct continuity of nodal and atrial-muscle fibres has not been established, but there is no definite boundary of the node; the fibro-muscular area which it forms gradually fades into the surrounding myocardium.

Vessels and Nerves of the Sino-Atrial Node.—The rich vascular supply of the node was pointed out by KEITH and FLACK and later was specially described by KOCH. The artery which passes through the substance of the node arises from an anastomoses (circulus arteriosus sinoauricularis, KOCH) between two branches of the right (or frequently one from the left) coronary artery (see p. 102); it serves as an additional guide to the node.

The node (monkey, man, MEIKLEJOHN) receives an extensive innervation from the ganglia immediately above it. The nerves break into fine fibrils which form a delicate plexus round the muscle fibres; they present a great variety of endings in the monkey, but no endings have been found in the human heart. No ganglion cells are present in the node.

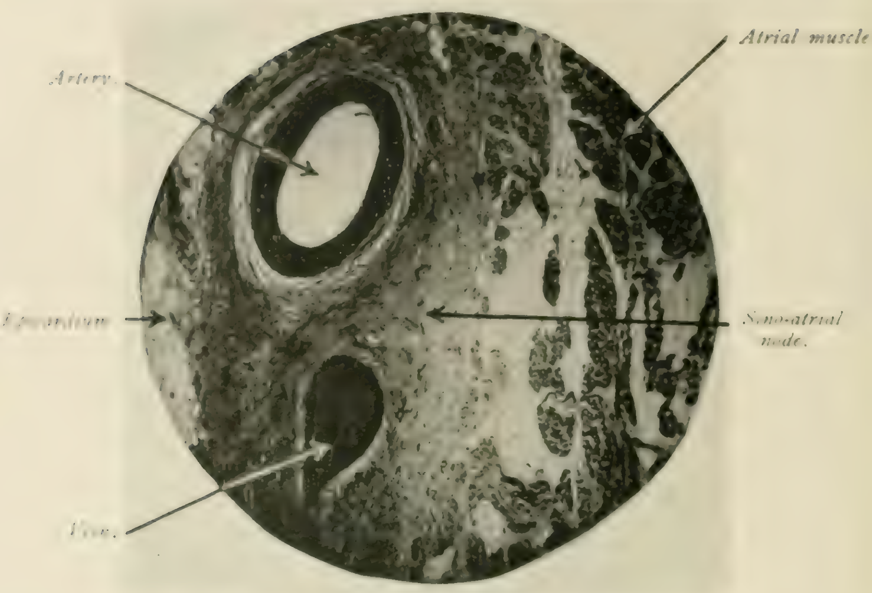


Fig. 60A.—The sino-atrial node of the human heart.
(Microphotograph, L.P.)

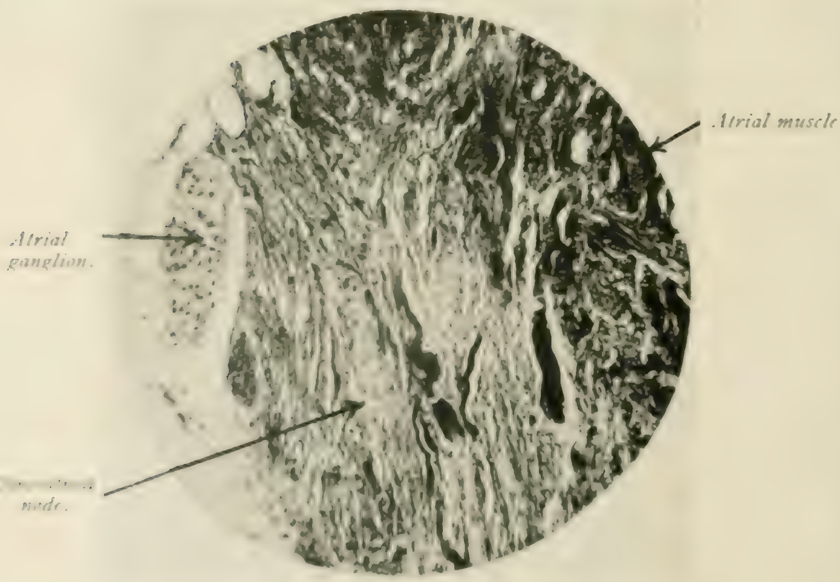


Fig. 60B.—The sino-atrial node of the human heart.
(Microphotograph, H.P.)

Exposure of the Sino-Atrial Node. The sino-atrial node may be exposed in a fresh adult heart by carefully removing the epicardium over the upper end of the sulcus terminalis, working from both sides towards the groove. The sub-epicardial fat should then be raised, again working from both sides towards the sulcus, and the muscle fibres of the superior cava and the neighbouring atrium, both of which have a definite course and arrangement, should be defined. Wenckebach's bundle will be exposed about the middle of the sulcus, and above it the node is usually easily recognised by its lighter colour and greater consistency and by the indeterminate direction of its fibres.

Purkinje Fibres of the Atrium.—Purkinje fibres in the atrium were first described by THOREL, and their free occurrence, especially on the septum and at the orifice of the superior and inferior cavæ was demonstrated by TANDLER; and their presence has since beeen confirmed by FREUND (in man), HOLMES (in the calf), SCHWARTZ and PACE (in several mammals), and in the ostrich (CLARK). KOCH and MÖNCKEBERG, however, have denied their presence. KOCH apparently worked only on children's hearts, and it should be noted that THOREL and TANDLER have expressly stated that they were unable to discover them before adult age (THOREL gives forty years and TANDLER twenty-eight years as the time of their appearance). MÖNCKEBERG holds that they are abnormal formations, but TANDLER found them "in absolutely healthy hearts and in isolated bundles among healthy muscle fibres at definite and constant parts of the heart." The present writer holds them to be proper formations of the adult heart (in man and the sheep), where they are to be found as broad pale fibres, larger than the atrial fibres, with characteristic fine, peripheral, longitudinal striation and a lighter, fibril-free, central zone in which lies the large oval nucleus; that is, they agree in all respects with the Purkinje fibres of the ventricle. THOREL held that these fibres form a complete system between the sino-atrial node and the atrio-ventricular node, but this description of a connecting path is not generally accepted. The fibres occur in long distinct bundles, which may or may not have fibrous sheaths, and in smaller or single-fibre groups set among the atrial muscle. The larger bundles occur at definite parts of the right atrium; for example, (1) in the neighbourhood of the atrio-ventricular node, but whether they are continuous with the node is uncertain; (2) at the lateral circumference of the orifice of the inferior cava; (3) round the orifice of the coronary sinus; and (4) along the junction of the posterior wall of the atrium with the septum (TANDLER). The smaller bundles would appear to be offsets of the larger bundles.

The Morphology of the Connecting Systems.—A discussion of the comparative anatomy and developmental history of the connecting systems of the heart is perhaps as yet hardly profitable. The facts are available, outside the mammals, only for a few forms in each of the great groups, and there are such differences in the descriptions, for example, among the fishes and the birds, as to indicate that there are wide differences in the arrangements in closely related forms and that no systematic comparative series can be established. Certain general conclusions, however, may apparently be drawn; but it appears to the writer that there are other considerations, for example the rate of conduction of the cardiac impulse, which are more important than a purely morphological comparison of the connections between the chambers of the heart, for they establish such distinctions between the hearts of lower and higher vertebrates that they vitiate a simple comparison between the structural conditions of the fish heart and the mammalian heart.

The discussion of the co-ordinated contraction of a chambered heart centres itself on the transmission of the excitatory process from chamber to chamber.

In a simple chambered heart it is obviously essential for the working of the heart that the transmission of the contraction from the contracting to the receiving chamber should be delayed at the junction between them, for only in this way will the receiving chamber be filled before it begins to contract. This statement, with a slight difference in the emphasis, is essentially similar to GASKELL's, namely, that the co-ordinated sequence of events in the cardiac cycle is due to a difference of rhythmicity and of conductivity in different parts of the heart, the conductivity being diminished at the junctions. It is found in the frog, for example, that the impulse passes over the sinus at the rate of about 100 mm. per sec. (CLARK) and then halts for ·2 to ·4 sec. at the sino-atrial junction; the rate of conduction is also about 100 mm. per sec. in the atrium and in the ventricle, and there are halts of about ·2 sec. at the atrio-ventricular and ventriculo-bulbar junctions. Figures of similar magnitude (100 to 200 mm. per sec.) express the rate of conduction in the sinus, the atrium, and the ventricle of other cold-blooded vertebrates, and in all there is a marked delay at the sino-atrio and atrio-ventricular junctions. The manner in which the delay is produced is not primarily a structural problem, but there seem to be at least three morphological factors concerned in it (or in its expression); namely, (1) the peculiar arrangement of the connecting muscle fibres; (2) the partial interruption by fibrous tissue of the muscular continuity between successive chambers; and (3) the specialised structure of the connecting muscle fibres.

(1) The arrangement of the connecting muscle fibres has been considered by SKRAMLIK (*Zeitsch. f. d. gesam. exp. Med.*, Bd. xiv., 1921), who has shown (in the frog) that the muscle fibres of the sinus, the atrium, and the ventricle are arranged in bundles which branch in all directions forming a basket network;[1] at the sino-atrial and atrio-ventricular junctions, however, he found that all the fibres are arranged in a circular ring, and in this respect they suggest a comparison with the sphincteric rings of the gut. SKRAMLIK accounts for the delay in conduction at these parts by supposing that the rate of conduction is inversely proportional to the number of cells per unit distance that the wave of excitation has to traverse; and this number is obviously greater at the junctions where the cells are arranged transversely to the direction of the wave of excitation. The sphincteric nature of the rings at the constricted parts of the primitive heart and in the early stages of development of the heart of higher vertebrates has already been suggested (pp. 4 and 61). It was then pointed out that the primitive mechanisms which close the orifices of the cardiac chambers consist of the sphincteric rings and the subendocardial swellings which they appropriate by their contraction. The evidences are (see below, fish heart) that a muscular arrangement constituting a virtual sphincter persists in lower vertebrates, but that in them, and in higher vertebrates where the sphincteric arrangement is not obvious, the sphincteric (connecting) musculature need no longer be actively contractile; for the primitive closing mechanisms are replaced by mechanically acting membranous valves derived from the subendocardial swellings. Contractility as well as conductivity, therefore, is diminished in the junctional musculature, while rhythmicity is enhanced.

(2) The conductivity is further diminished, even in cold-blooded vertebrates, by the considerable amount of connective tissue at the atrio-ventricular junction, so that the number of muscle fibres connecting the atrium and the ventricle is relatively small. The "narrowing" of the junction thus produced between the two parts, it is well known from numerous records, reduces the rate

[1] For the details of the arrangement, see SHANER, *Journ. Anat.*, vol. lviii., 1923.

of conduction (and induces a long refractory period, ENGELMANN): and by partial section of the remaining connection the rate may be still further reduced (GASKELL). It is found, therefore, on examination, that the atrio-ventricular connection has a lower conducting power than the musculature of the atrium or of the ventricle; for ECKSTEIN (*Pflüger's Arch.*, Bd. clvii., 1914) has shown that either the atrium or the ventricle can be driven at a more rapid rate than the connection can transmit impulses, and that, therefore, either an atrio-ventricular or a ventriculo-atrial block can be induced.[1] It may also be added that atrio-ventricular conduction is more readily influenced by drugs or changes in ionic concentration than is the conductivity of the atrium or the ventricle; as already pointed out there are differences in the glycogen content.

(3) The histological structure of the connecting muscle fibres is the feature to which most attention is now given. The details of the specialisation, as already described, present considerable differences in different forms, but the common basic characters may be summarised as a very incomplete longitudinal striation, a large protoplasmic content, and a central position of the rounded nucleus in syncytial fibres of some length; and if any reliance at all is to be placed on the meaning of details of structure then these fibres are not so actively contractile as the general myocardium, and the difference in structure can only mean that they exist for a distinct purpose. It may be interpolated here that the structure described is not simply the retention of the characters of embryonic heart muscle; as will be fully appreciated from the developmental history (p. 97), it is a distinct specialisation of structure. A rich vascular supply is characteristic of the connecting tissue and, more significantly, it is accompanied at all parts by large numbers of nerve fibres; the participation of nerve fibres, and at some parts of nerve cells, in the composition of the tissue is so great, and nowhere is it greater than in the fish heart (MACKENZIE), that it is often referred to as a neuro-muscular tissue.

The specialised tissue now described, of high rhythmicity and low contractility and conductivity, in close connection with the nervous system, and localised round the sphincteric parts of the heart since it is derived from them, is represented in all vertebrates; with increasing complexity of the organ its conformation changes, but its general relations remain the same and, it may be claimed, it is a homologous structure throughout. The arrangements in the lower vertebrates now fall to be briefly described. The details are largely taken from MACKENZIE'S work on the comparative anatomy of the connecting system.

Fish.—At the sino-atrial junction there is, along the bases of the sinus valves, a ring of loose, richly protoplasmic, and poorly striated muscle fibres. These fibres are continuous with the inner of the two muscular layers of the venous valves, the outer layer of the valves being continuous with the cortical atrial muscle (fig. 61). The fibres, it is well to note, though they are in the sinus region of the heart and as far as is known are developed from the same primordium, are not sinus muscle or the remains of sinus muscle; they are specialised structures of their own kind. The right and left nerve trunks to the heart reach the sino-atrial junction as single trunks, but at the basal attachment of the venous valves they break up into small branches which encircle the sino-atrial orifice; from the network numerous branches enter the sino-atrial ring and others pass to the general musculature of the atrium. There are several ganglion cells scattered in the network, but they are found in larger numbers opposite the

[1] It has been repeatedly shown, of course, that the rate of atrio-ventricular conduction is greater than the rate of ventriculo-atrial conduction.

ends of the valves and at the base of the dorsal cusp. The atrial musculature is continuous with the ventricular musculature through a ring of specialised fibres of small size. This ring lies on the outside of the atrio-ventricular valves and is continued down on the inside of the ventricle wall beyond their basal attachment (fig. 61). There are only a few nerve fibres in the atrio-ventricular groove.

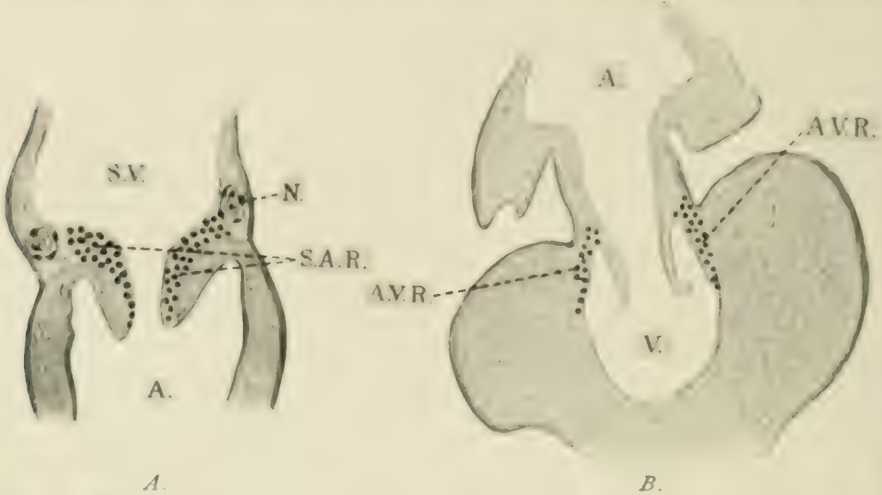


FIG. 61.—THE CONNECTING SYSTEMS OF THE FISH HEART. (After MACKENZIE.) *A*, THE SINO-ATRIAL RING, AND *B*, THE ATRIO-VENTRICULAR RING.
A., atrium: S.V., sinus venosus; V., ventricle; N., nerve plexus.

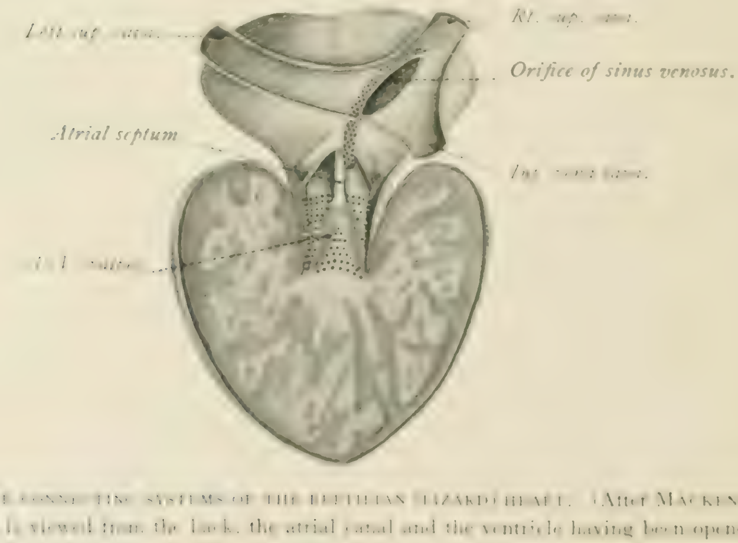


FIG. 62.—THE CONNECTING SYSTEMS OF THE REPTILIAN (LIZARD) HEART. (After MACKENZIE.)
The heart is viewed from the back, the atrial canal and the ventricle having been opened.

In some forms (the ling, MACKENZIE) the anterior and posterior parts of the ring have disappeared, and there persist only two strands of specialised muscle opposite the ends of the valves.

Reptiles[1].—In the lizard's heart (fig. 62) specialised muscle is present at

[1] There is a considerable "smooth muscle" connection between the chambers of the heart in reptiles, but this is not discussed here.

the sino-atrial junction only along the base of the left venous valve. At its lower end this mass is continued into a broad band, apparently of the same structure, which descends to the back of the atrio-ventricular ring, lying in part of its course behind the sinus and the atrium entirely free from the cardiac muscle (MACKENZIE).[1] This connection between the sino-atrial and atrio-ventricular rings is absent in the crocodile.[2] The atrio-ventricular ring of specialised muscle descends on the inner face of the ventricle as far as the lower attachment of the atrio-ventricular valves (the upper ends of which are attached to the lower end of the atrial septum). In front the ring is continued on to the bulbo-atrial ridge, but otherwise it is carried down only into the left ventricle. In the crocodile, however, where the interventricular septum is complete (p. 9), the back part of the ring is carried forward on its summit, below the membranous part of the septum, and is distributed in part to that portion of the right ventricle which corresponds to the part of the human heart which in this work has been termed the " inflowing " part.

Mammals.—In mammals the sino-atrial node, a typical neuro-muscular mass, is invariably found at the base of the upper part of the right venous valve. The explanation of the presence of the right and the absence of the left valve ring is probably to be sought in the fusion of the left venous valve with the atrial septum and the disappearance of the spatium intersepto-valvulare (p. 40), and in the interruption of its basal part by the development of the limbic bands (p. 40). It has been stated by RETZER, however, that in the pig embryo the left valve carries down specialised tissue to the atrio-ventricular ring; but the concept of the morphology of the specialised muscle given by RETZER differs so much from that advanced in this work that only mention of it is made here. Further work is needed on the sino-atrial tissue of the hearts of monotremes and marsupials. The distribution of the atrio-ventricular system is more complex. This system has been described to consist of the following parts: (1) the atrio-ventricular node of TAWARA; (2) the atrio-ventricular bundle of HIS and its branches; and (3) the network of the fibres of PURKINJE. Structurally two regions of the system have been distinguished: (1) an atrial part, the neuro-muscular node of TAWARA, the fibres of which are small, richly protoplasmic, freely commingled, and embedded in a fibrous reticulum; and (2) an atrio-ventricular part, the bundle of HIS and the fibres of PURKINJE, the fibres of which vary in their size and in the amount of difference between them and the fibres of the myocardium. It has also been shown (LEWIS, *Proc. Roy. Soc.*, B. lxxxix., 1917) that the rates of conduction of these two parts (in the dog) are strikingly different, as is expressed in the following table:—

DOG.	*Rate of Conduction.*
Atrium	800 mm. per sec.
A.V. node	200 ,, ,, (or less).
Purkinje fibres	4,000 ,, ,,
Ventricle	400 ,, ,,

The nature of the node would thus seem to be well established; structurally and functionally it is homologous with the sino-atrial node, and both represent parts of the primitive specialised junctional tissue of the heart, of low contractility, low conductivity, and high rhythmicity, and in intimate connection with the

[1] This is the ligamentum atrio-ventriculare of DOGIEL, who maintains it is a neural connection, and the dorsal ligament of LAURENS, who holds it to be a pericardial fold serving as a pathway for vessels and nerves and containing numerous ganglion cells.

[2] It is also absent in the alligator (SWETT, *Anat. Record*, vol. xxvi.).

nervous system. The origin of the node is not as yet decided, that is whether it is part of the sino-atrial ring or part of the atrio-ventricular ring. It has already been held in this work (p. 41) that it lies in the proper atrial region of the atrium, that is outside the area enclosed by the sinus valves (see also a diagram by KEITH, *Lancet*, 1906), and that it is, therefore, part of the atrio-ventricular ring. There is some experimental support,[1] however, for the view that it is part of the sino-atrial ring, or, more particularly, the lower end of the sino-atrial band as is present in the lower reptiles (fig. 62), and, further, it is stated by MACKENZIE that in the kangaroo it lies within the limits of the venous valves. The atrio-ventricular part of the system (the bundle of HIS and the network of PURKINJE) are derivatives of the atrio-ventricular ring, the modification

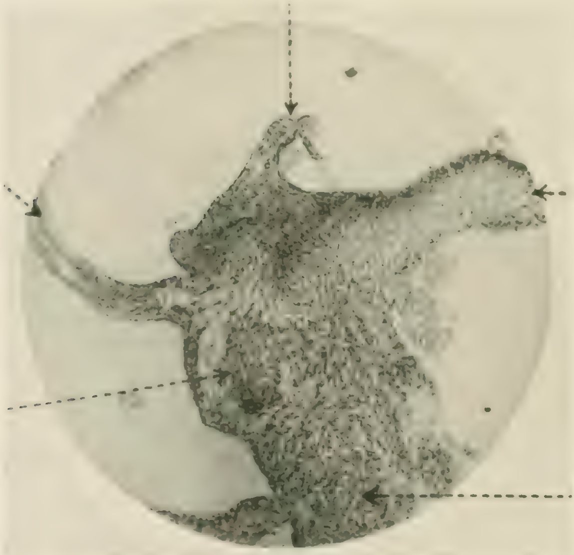


FIG. 63.—THE ATRIO-VENTRICULAR BUNDLE OF A HUMAN EMBRYO OF 19·75 C.R. LENGTH. (Microphotograph.)

in its form representing a reduction ("narrowing"), a displacement forwards on the ventricular septum, and an extension of the distribution on the ventricle walls, of the primitive funnel-shaped ring. The reduction of the ring to a single band has already been associated with the development of membranous valves, and the displacement forwards with the completion of the ventricular septum; the wide extension of the terminal network, more dense in the apical than in the basal part of the ventricles, is a mammalian acquisition and ensures the conduction of the impulse to all parts of the ventricle.

Birds.—The mechanism of the heart of birds is different from the mechanism in mammals. The rates of conduction in the atria and ventricles are much higher (2,000 to 4,000 mm. per sec.). The arrangement of the connecting

[1] The experimental evidence is that the right vagus and sympathetic seem to be chiefly associated with the sino-atrial node and the left vagus and sympathetic with the atrio-ventricular node, and the two nodes are considered to be the right and left parts of the sino-atrial ring.

systems is peculiar, but they are not absent as is sometimes described (MACKENZIE and ROBERTSON, KEITH). There is a Purkinje network in the atrium (ostrich) and in most parts of the ventricles (hen) (see fig. 58), and a description of the macroscopic dissection of the atrio-ventricular bundle (in the ostrich) has been given by DRENNAN. The description of the details, however, need not be given here. (See TANG, *Anat. Anz.*, Bd. lv.)

The Development of the Connecting System. The developmental history of the connecting system is by no means yet fully known. It has been studied in the pig by RETZER and in the human heart by TAWARA, MÖNCKEBERG, TANDLER, and MALL. RETZER describes the appearance of the atrio-ventricular system at the same time as the formation of the septum primum, but he describes the origin of the whole system from the left venous valve. TANDLER was able to recognise the bundle of His in a 10 mm. human embryo on the posterior wall of the atrial canal as a strip of cells of darker colour. At this stage the atrial and ventricular musculatures are continuous with one another at the atrial canal, so that the bundle cannot be considered simply to represent a remaining part of this canal after the union between the musculatures has been interrupted, but is already at the 10 mm. stage a differentiated structure. In a human embryo of 19·75 mm. length, the bundle of His can be recognised on the summit of the ventricular septum; its appearance, the nuclei being very dark and the protoplasm poorly staining, is not unlike that of the "anlage" of a sympathetic ganglion, only it is poorer in the number of cells (fig. 64). The right and left limbs can be traced for a short distance in this specimen; in a 28 mm. embryo they can be followed much further. MALL has stated that the bundle can be recognised in a 7 mm. embryo; it is separated from the surrounding tissue by a distinct space and is found on the posterior wall of the atrial canal, under the endocardial cushion,[1] approximately at the place at which the atrial septum reaches it. In later stages, 20 mm., it shows the differential staining and its two limbs can be found. It cannot be followed upwards on the posterior wall of the atrium to the sinus. At the 20 mm. stage the separation of the cortical ventricular muscle and the atrial muscle is complete (p. 59), and the atrio-ventricular bundle represents the sole union between the two. (Other persistences between the atrium and ventricle described by PALADINO and KENT have been referred to (p. 78); MALL describes them as possible variations.) In later stages the muscular differentiation becomes more marked, the connecting system being more lightly coloured; and at the 35 mm. stage it can be recognised to consist of short cells, fused with one another, in which longitudinal striation is just apparent (MÖNCKEBERG).

The developmental history of the sino-atrial system is unknown.

The **connecting systems** of the **mammalian heart,** as now described, are believed to be derived from the primitive junctional sphincteric rings between the sinus and the atrium and the atrium and the ventricle, and they cannot, therefore, be considered as primitive sinus, or primitive atrial muscle. Two lines of development have been followed, so that the systems of the adult consist of two distinct tissues: (1) the nodal tissue of the sino-atrial and atrio-ventricular nodes, and (2) the atrio-ventricular bundle and its terminal ramifications, the fibres of Purkinje. The nodes are neuro-muscular structures of high rhythmicity, and at present are probably best looked on as cardio-regulatory centres of the atria and ventricles respectively, initiating the contractions of these parts, but co-ordinated through the nervous system; how far they are comparable to such tissues as the myenteric

[1] The part of the trigonum which the bundle perforates is developed from this region.

plexuses cannot yet be stated. The atrio-ventricular bundle, it has been seen, is differentiated at a time when atrio-ventricular continuity is intact and develops along its own lines. It must be concluded, therefore, that it is a structure of great functional importance and more than merely a bundle of muscular continuity; it undoubtedly belongs to the motor apparatus of the heart. It possesses, on the one hand, characters of muscle,[1] and on the other similarities to nerves,[2] so that it is difficult to class it with the one or other tissue; it probably must be looked on as a distinct tissue, not to be subsumed under any other, and to be the distributing tissue to the ventricular muscle of the impulse of contraction from the node of Tawara. Its true nature, however, is still a matter to be decided, and the possibilities, for example, of its resemblance to the longitudinal muscle of the gut, cannot yet be discussed in a text-book.

THE BLOOD VESSELS OF THE HEART

The **arteries** which supply the heart are two comparatively small vessels, the **right** and **left coronary arteries**, which arise from two of the sinuses of Valsalva at the commencement of the aorta. They belong, therefore, to the visceral systemic circulation, though they differ from the other visceral arteries in many respects.

The **right coronary artery** (figs. 64, 65) arises from the anterior sinus of Valsalva and proceeds directly to the right. It appears on the surface of the heart between the pulmonary artery and the right auricular appendix and, embedded in fat, runs in the coronary sulcus round the margo acutus on to the posterior aspect of the heart; on this aspect it usually extends as far as the posterior interventricular groove, where it divides into two branches. The smaller branch continues to the left in the coronary sulcus, approaching the termination of the transverse branch of the left coronary artery, and ends by dividing into two or three branches, **rami ventriculares sinistri**, which descend on the posterior surface of the left ventricle; while the other branch, **ramus descendens posterior**, descends in the posterior interventricular furrow and gives off branches to both ventricles and others which pass forwards into the interventricular septum (fig. 65). In its course the artery gives off the following branches:—

(1) An **infundibular** branch which ramifies over the front of the conus arteriosus and anastomoses with a corresponding branch of the left coronary artery. In 33 per cent. of bodies this branch arises directly from the anterior sinus of Valsalva (BANCHI). (2) Two main branches which descend on the anterior surface of the right ventricle, giving off a number of more or less parallel horizontal twigs; these extend to the right as far as the margo acutus and to the left to meet similar branches from the left coronary artery. (3) A constant stout

[1] It is generally believed that the atrio-ventricular bundle is non-contractile, and also that it does not participate in atrophic or hypertrophic changes of the myocardium; CURRAN, however, does not completely agree with the latter statement, and as already pointed out (p. 78), he has described movements of the right limb of the bundle in the ox. Studies of the bundle with polarised light strengthen the view that the fibres of the bundle possess moderate powers of contractility (JOHNSTONE, *Anat. Record*, vol. xxvi.). It has been stated that rhabdomyomata of the heart consist of Purkinje fibres (RETZER, *Anat. Record*, vol. ii., p. 158). There [illegible] no adequate evidence to support RETZER's suggestion that "worn out myocardium is replaced from the Purkinje system."

[2] That it is not simply a motor nerve, though perhaps comparable in function, is shown by the fact that it does not undergo degeneration below the place of section (KEITH).

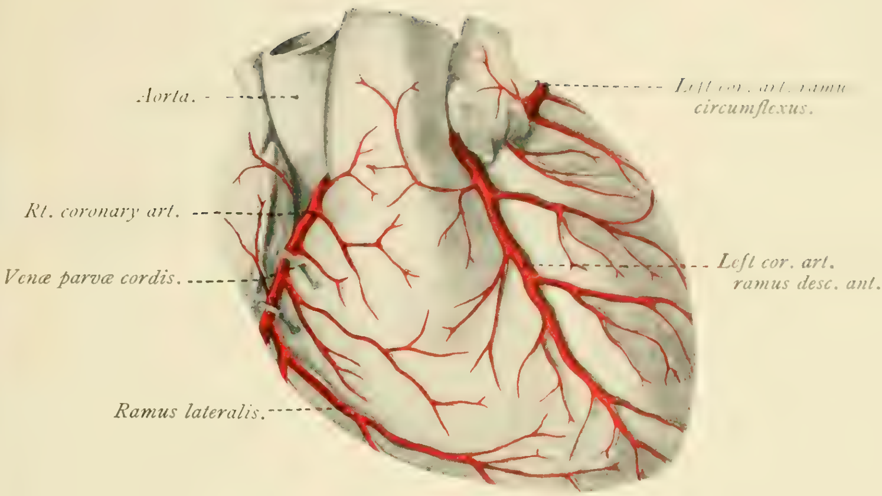


FIG. 64.—THE CORONARY ARTERIES ON THE FRONT OF THE HEART.

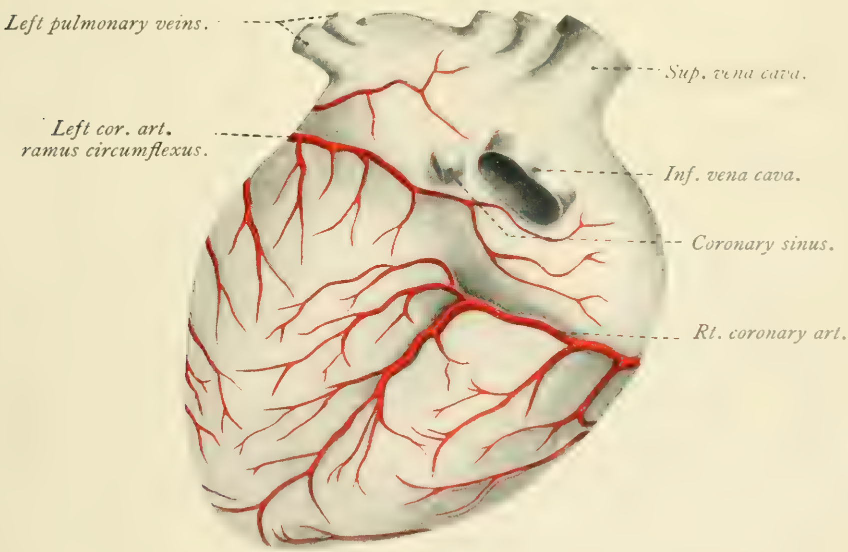


FIG. 65.—THE CORONARY ARTERIES ON THE BACK OF THE HEART.

(The terminal atrial branch of the left coronary artery is, in this specimen, larger than usual.)

lateral or marginal branch, **ramus lateralis**, which descends along the margo acutus giving offsets to the anterior and posterior surfaces of the marginal part of the right ventricle. On the lower third of the ventricle it often turns backwards and runs transversely across the inferior surface to reach the posterior interventricular groove (GROSS). (4) Smaller and inconstantly placed branches, three or four in number, are given to the right atrium in front and behind (see below), while several delicate twigs, constantly found and remarkably regular in position, are distributed to the roots of the aorta and pulmonary artery. (See "Comparative Anatomy of Coronary Arteries.")

The **left coronary artery** (figs. 64, 65, 66), generally rather larger than the

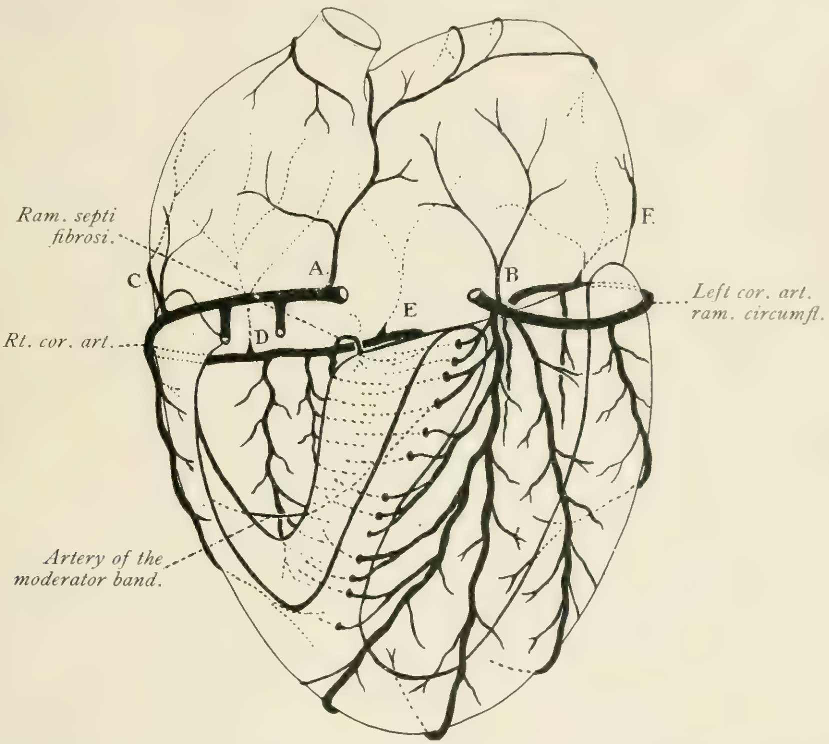


FIG. 66.—A SCHEME OF THE DISTRIBUTION OF THE CORONARY ARTERIES. (After CAMPBELL.)

right artery,[1] arises from the left sinus of Valsalva. It passes behind the pulmonary artery and then forwards between that vessel and the left auricular appendix, in which position, after a course of about half an inch, it divides into two branches. The larger branch, **ramus descendens anterior**, appears on the anterior surface of the heart and descends in the anterior interventricular furrow to the lower margin of the heart, round which its terminal branches pass

---

[1] The two vessels are, as a rule, different in size, but while KRAUSE, CRUVEILHIER, and ALBRECHT describe the right vessel to be more often larger than the left, in a recent examination by HALBERTSMA the left vessel was, as is stated above, more often larger than the right; the left was more often the larger vessel in the writer's series. In some quadruped mammals (ox) the difference between the two vessels is very great. A marked diminution in the size of one coronary artery is compensated by an increase in the other, which then is distributed over a larger part of the heart (see below). The calibre of the coronary arteries, especially when diseased, may vary suddenly.

to gain the diaphragmatic surface. There arises from this vessel, near its origin, a branch which ramifies on the conus arteriosus, and throughout its course it gives numerous transverse branches to the anterior surface of the right ventricle and a series of larger and fairly constant branches, **rami collaterales**, which run more or less parallel to one another downwards and to the left on the left ventricle, while from its deep surface branches pass from it into the inter-ventricular septum, the uppermost of the series being large and easily defined (fig. 66). The second branch, **ramus circumflexus**, runs to the left in the coronary sulcus and becomes superficial about the margo obtusus round which it passes on to the diaphragmatic surface. It extends on this surface for a varying distance towards the right, but only seldom does it reach the posterior inter-ventricular furrow; and it ends by turning downwards on the left ventricle. In its course it gives off branches to the anterior and posterior surfaces of the

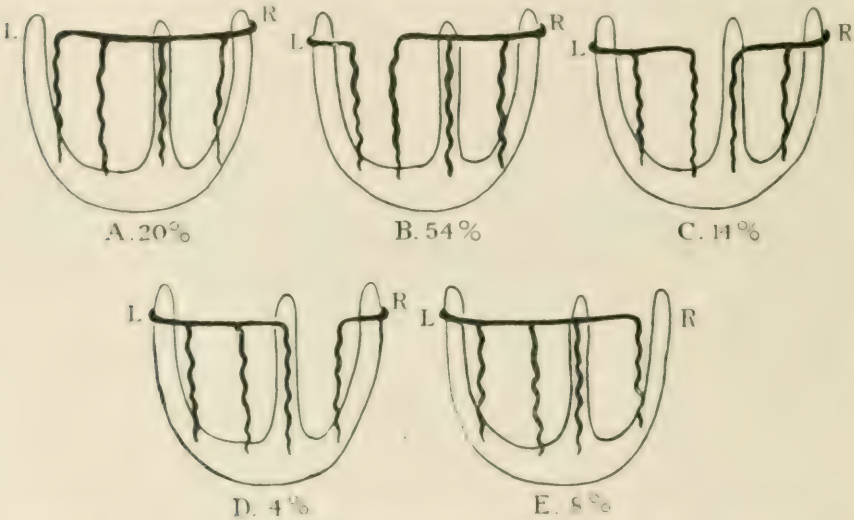


FIG. 67.—AN ANALYSIS OF THE DISTRIBUTION OF THE CORONARY ARTERIES ON THE BACK OF THE VENTRICLES. (After CAMPBELL.)
R. and L., right and left coronary arteries.

left atrium (see below) and left ventricle, most of which are unnamed, but usually constant among them are a branch to the anterior surface of the atrium, **ramus atrialis anterior**, a branch which accompanies the vein of Marshall, and one or two branches which descend on the margo obtusus, **rami marginales**. The left coronary artery, at its beginning, supplies small branches to the root of the aorta and pulmonary artery.

Variations.—The level of the orifices of the coronary arteries in the sinuses of Valsalva varies in both vertical and horizontal directions. Most commonly they lie at the level of the free edge of the cusp, but they are often above this level (Vischia claims this position to be the most common) and in a few instances below it; and while most commonly at the centre of the sinus they are often found nearer its anterior margin. The two coronary arteries have been seen, though in only a few instances, to arise by a common trunk or both to arise from one sinus of Valsalva (Morgagni, Cruveilhier, Hyrtl, Bochdalek, Engelmann). Not infrequently the number of coronary arteries is increased to three and in a few instances four have been observed. The supplementary vessels are generally small (and probably are often overlooked, for Symmers, *Jour. Anat.*, vol. xli., found them in 40 of 100 hearts examined); they spring from the aorta near the main coronary trunk, of which they represent normal branches which have acquired an independent origin. They occur on both sides, but probably more frequently on

the right side. In very rare instances an additional coronary artery has been found arising from the pulmonary trunk (KRAUSE, BROOKS, HEIDLOFF).

Distribution of the Coronary Arteries.—The chief **ventricular** branches of the coronary arteries lie on the surface of the heart embedded in fat and covered by the epicardium; sometimes they are bridged over by a few muscle fibres. They show not inconsiderable variations in their number and course and in the area of the heart wall they supply. They are specially variable on the back of the heart, where the left artery may furnish the branch descending in the posterior interventricular furrow or the right artery may supply the whole posterior surface of the heart as far as the margo obtusus. (For a detailed account of these variations reference may be made to GROSS and CAMPBELL: an analysis of fifty injected hearts of CAMPBELL'S series is given in fig. 67.) The secondary branches ramify on the surface of the heart for most part at right angles to its long axis, and from them the finer branches pass into the heart muscle (fig. 70B). In the myocardium the general direction of the arteries is inwards (towards the endocardium) through the successive muscle layers, the vessels gradually diminishing in size as they approach the inner surface. The adventitial coat is very much reduced when the vessels

FIG. 68.—THE ARTERIES OF THE SEPTUM.

X-ray photograph of the injected arteries; from a specimen prepared by J. S. CAMPBELL. The anastomoses between the anterior and posterior septal arteries are shown.

enter the myocardium. The ultimate capillary formation is a long narrow meshwork in the direction of the muscle fibres, parallel capillaries connected by short transverse branches lying in the intervals between individual fibres (KÖSTER); MEIGS has demonstrated the presence of very large vessels of capillary structure, and he also has stated that the capillaries penetrate the muscle fibres, but this has not been confirmed. The arteries for the papillary muscles enter them at their base and divide into branches which ascend to the apex of the muscles, in their course being connected by transverse branches (RIBBERT). The arteries of the interventricular septum are branches of the anterior and posterior interventricular trunks and run backwards and forwards in it parallel to the base of the heart (fig. 68). The uppermost of these, **ramus septi fibrosi**, arises (usually) from the transverse branch of the right coronary artery and supplies the area round the orifice of the coronary sinus and the upper back part of the ventricular septum (see "Blood Supply of Atrio-Ventricular Bundle"); if the left artery extends on to the right side of the heart this branch arises from it (fig. 67). It perforates the trigonum dextrum behind the atrio-ventricular bundle.

The **atrial** branches of the coronary arteries are less constant in their arrangement than the ventricular arteries. Six or seven fairly constant stems are present, ramifying over both surfaces of the atria and anastomosing freely with one another, but any one, or any combination of two or more, may be much larger than the others and become the chief atrial blood supply. The

commonest arrangement in CAMPBELL's series is shown in fig. 67; it occurred in 39 of the 70 specimens. Six stems are shown, four from the right coronary artery and two from the left vessel. The first branch of the right artery, which arises near its commencement, passes upwards on the anterior wall of the right atrium, where it anastomoses with the first branch of the left artery. It gives off branches which pass into the atrial septum, some of which turn downwards and anastomose with twigs of the ramus septi fibrosi, and others of which ramify over the anterior wall and roof of the atria. The main stem continues over the roof of the right atrium to the posterior surface of the superior vena cava and there it terminates in a ring-like plexus round its orifice; from this plexus one large branch descends in the sulcus terminalis and supplies the tissue of the sino-atrial node. In the second most common arrangement (present in twenty specimens in CAMPBELL's series) the branch (A) from the right coronary artery is small and that (B) from the left coronary artery is large, and through the corresponding anastomoses reaches the caval orifice and forms the ring-like plexus (see fig. 70, B); in the remaining specimens one of the other branches (C, D, E, F, but more commonly F or C, and rarely D or E) is the chief atrial

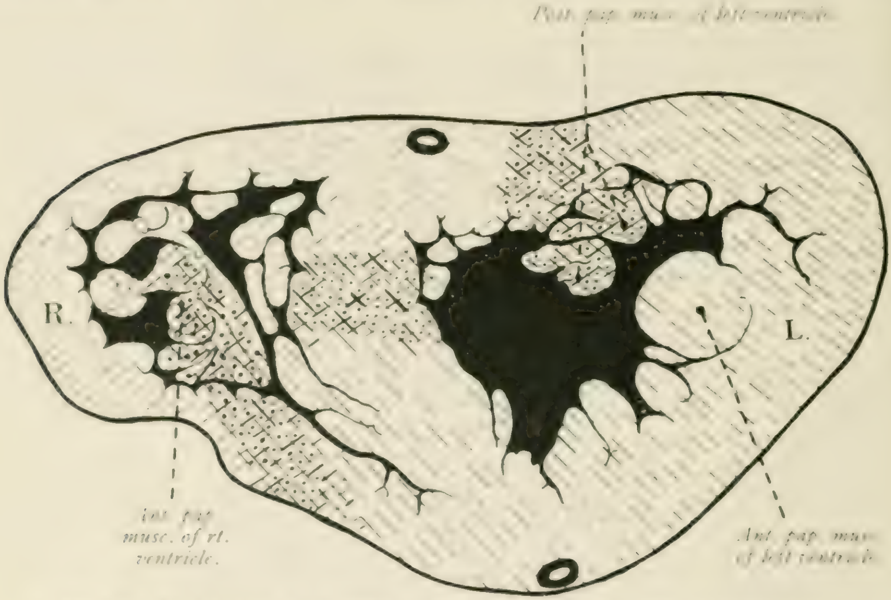


FIG. 69.—A DIAGRAM TO SHOW THE USUAL AREAS OF DISTRIBUTION OF THE CORONARY ARTERIES. (After TANDLER.)

R. and L. are placed in the shadings which correspond with the areas of distribution of the right and left coronary arteries respectively; the areas supplied by both arteries are cross-hatched. (Compare with fig. 67.)

vessel and forms the plexus. (A very full discussion of the atrial blood supply is given by SPALTEHOLZ.)

In addition to the branches to the myocardium described above, the coronary arteries and their branches give off a large number of twigs, **arteriæ telæ adiposæ cordis**, which ramify as a rich network in the subepicardial fat and supply it. These vessels can be satisfactorily identified only in cleared specimens. The vessels which ramify on the surface of the root of the aorta and pulmonary artery belong to this group.

The **areas of distribution** of the coronary arteries have been determined by coloured injections (AMENOMYIA, STERNBERG, NUSSBAUM), by injected and cleared hearts (SPALTEHOLZ), and by X-ray photographs of opaquely injected specimens (GROSS), and it has been shown that, apart from individual variations, fairly well-defined regions of the ventricles are supplied by each of the vessels while other parts are supplied by both arteries (fig. 69); the atrial distribution, as stated above, is more prone to variation and a typical description cannot be given of it. The right coronary artery supplies the whole of the right ventricle with the exception of the left third of the anterior wall. It supplies also the posterior part of the interventricular septum and the posterior wall of the left ventricle as far as the attachment of the posterior papillary muscles, in the supply of which it shares. The left coronary artery supplies the remainder of

the left ventricle, the anterior part of the septum, and part of the anterior wall of the right ventricle, and shares in the supply of the anterior papillary muscle of the right ventricle by a distinct branch (which can easily be dissected) which passes along the moderator band (fig. 66).

Anastomoses of the Coronary Arteries. The question of the pre-capillary anastomoses of the coronary arteries has long been a matter of discussion and on it there is now a considerable literature; this has been fully summarised by Tandler, Spalteholz, and Gross. It may be simply stated here that, as the result of many different methods of anatomical and experimental investigation, it can no longer be held that the coronary arteries are "end arteries" in the sense that Cohnheim, in the support of Hyrtl and Henle, described them to be, that is, that there are no pre-capillary anastomoses; and this must be maintained even though Cohnheim's view has since been largely accepted on the strength of the pathological findings in infarction. On the contrary, it may be held to have been shown by a large number of workers that—

(1) There are anastomoses between the two coronary arteries and between the branches of each coronary artery, on the surface of the heart, in its substance, and immediately under the endocardium; and

(2) there are anastomoses between the coronary arteries and the vessels of adjacent parts, namely, the pericardial, diaphragmatic, and bronchial arteries.

The most recent methods, by radiographing injected coronary arteries (Jamin and Merkel, Gross, Campbell), and by clearing the heart after injecting the vessels (Spalteholz), have shown that there are great individual differences in the amount of the anastomoses; that there are considerable age-changes in the extent and the width of the anastomoses; and that the anastomoses may be increased in pathological specimens of obliterative endarteritis. The anatomical anastomoses being proved, the formation of infarcts in the heart, which postulates that the anastomoses is not functionally realised, requires to be explained. There has been formulated, therefore, by Pratt, a definition that an artery may be classified as a "functional end artery" if the resistance in the anastomoses is greater than the blood pressure in the anastomosing vessels; and to some extent at least the anastomoses of the heart may fall under this definition. Modern experimental work, however (Hirsch, Smith, Oppenheimer, Rothschild, Herrick, Gross, Galli), seems to show that factors other than that of anatomical arrangement decide the occurrence of infarcts, and that the age of the individual and the rate of the obliteration of the vessels are of great importance; and that the arteriæ telæ adiposæ may play a considerable part in establishing a collateral circulation in the heart of an aged person.

It should also be mentioned that Nussbaum has described direct arterio-venous anastomoses on the surface of the heart. He states that in the walls of the connecting vessels there are no muscle elements, and he concludes, therefore, that they are dilated capillaries; Meigs has also described these vessels.

Age Changes in Coronary Circulation.—There are, it would appear even from a small series of observations, well defined and fairly regular age changes in the coronary arteries. These may be described as follows (Gross): (1) There is an increasing tortuosity of the vessels, the tortuosity commencing in the third decade of life and increasing progressively; after the seventh decade it is accentuated by the general atrophy of the heart muscle. (2) There is an increasing relative anæmia of the right side of the heart. At birth and for some time afterwards the coronary arteries are distributed in equal density on the

FIG. 70A.—THE CORONARY ARTERIES AT BIRTH.

X-ray photograph of the injected coronary arteries of a newborn child; from a specimen prepared by J. S. CAMPBELL.

FIG. 70B.—THE CORONARY ARTERIES IN THE ADULT.

X-ray photograph of the injected coronary arteries in a male æt. 51; from a specimen prepared by J. S. CAMPBELL. A., first atrial branch of right coronary artery; B., atrial branch of left coronary artery [illegible] the [illegible] plexus. R.P., round the superior cava (cp. fig. 66); X., a ventricular branch of the right coronary artery arising alone.

two sides of the heart (fig. 70), but with the increased activity of the left ventricle there is a richer expansion of its blood supply than occurs over the right ventricle; and this relative anæmia of the right side, commencing definitely about the end of the second decade, increases progressively with the age (fig. 70). (3) There is an increase in the amount and the width of the anastomoses of the branches of the coronary arteries; the anastomoses in the ventricular septum can be detected in injected specimens in the second decade and increases very markedly in later life. (4) There is increasing development of fat vessels (rami telæ adiposæ) commensurate with the increase in the subepicardial fat. They form a dense subepicardial network in the later decades and may establish connections with the myocardial vessels and assist in the supply of the myocardium.

The **veins** of the heart may be conveniently arranged in three groups: (1) The great veins of the heart, **venæ magnæ cordis**; (2) the small veins of the heart, **venæ parvæ cordis**; and (3) the smallest veins, **venæ minimæ cordis**. All of them are subject to considerable variation.

1. **Venæ Magnæ Cordis** (fig. 71).—The great cardiac veins comprise a series of which the main vessels lie on the surface of the heart under the epicardium and open into a common trunk, the **coronary sinus**, which pours its blood into the right atrium. The main trunks accompany the coronary arteries, occupying a position side by side or superficial to them; their smaller ramifications, however, may be deep to the arteries. In the myocardium the veins are delicate tortuous channels, vessels up to ·25 mm. in diameter having capillary endothelial walls; they join one another close to the surface of the heart and open abruptly into the larger superficial trunks. The cardiac veins are devoid of valves in their course, but at their junction with the coronary sinus, with the exception of the oblique vein of Marshall (vena obliqua), they are provided with more or less complete one-cusp valves.

A. The **coronary sinus**, a short thick trunk about an inch in length, lies on the back of the heart in the left part of the coronary sulcus. It receives as its tributaries the great veins from the surface of the heart and it terminates by opening into the right atrium immediately in front of the inferior vena cava, the orifice being covered by the Thebesian valve. The definition of the left end of the sinus has been the subject of considerable discussion; it is generally considered to be, however, at the entrance of the left (or great) cardiac vein, the junction being indicated in the interior of the vessels by the valve of the vein (the valve of Vieussens).

The **coronary sinus** is sometimes placed above the coronary sulcus and then usually forms an arch, concave downwards, over the posterior surface of the left atrium. The transition from the left cardiac vein to the sinus is more often gradual than sudden, but, according to Gruber, a sudden dilatation at the commencement of the sinus is more typical in the fœtus and the child. The wall of the sinus is completely surrounded with transversely placed cardiac muscle fibres, which are, of course, absent from the walls of its tributaries; frequently, however, cardiac muscle fibres are absent from the distal part of the sinus. A few longitudinal fibres, prolonged on to it from the atrium, have also been described on the sinus wall.

B. The **left** (or great) **cardiac vein** (vena cordis magna) commences as the anterior interventricular vein near the apex of the heart, where it forms anastomoses with the corresponding posterior vein, and ascends, gradually increasing in size, in the anterior interventricular groove in company with the anterior interventricular branch of the left coronary artery. At the coronary sulcus it turns to the left, and, under cover of the left atrial appendix, winds round the margo obtusus; and having gained the posterior surface of the heart it terminates in the left end of the coronary sinus, the opening being guarded by a valve.

the valve of Vieussens, which sometimes is formed by two cusps. In the first part of its course it receives numerous branches from the interventricular septum and from the anterior wall of the left ventricle, and smaller branches, including some from the conus, from the front of the right ventricle; and as it passes backwards it is joined by descending branches from the left atrium and by ascending branches from the left ventricle, one of which, **vena marginalis sinistra**, lying along the left margin of the heart, is of considerable size.

C. The **posterior interventricular** (or middle cardiac) **vein** is of considerable size. It commences at the apex of the heart, where it communicates with

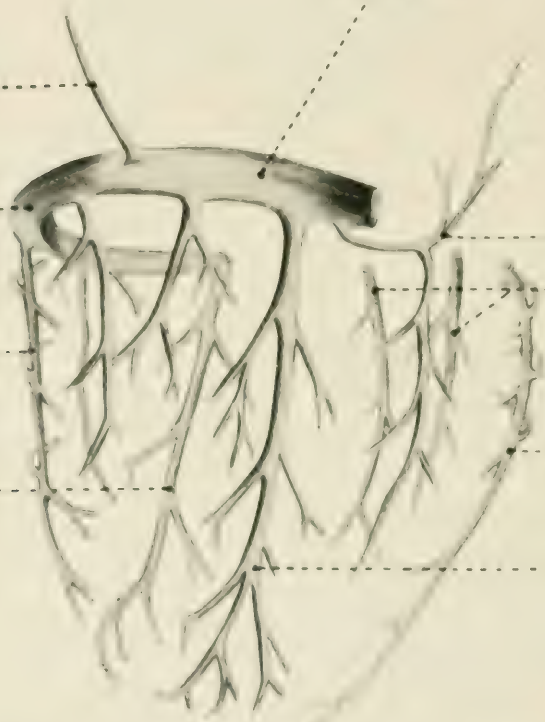


Fig. 71.—A diagram of the veins of the heart, from behind.

the radicles of the anterior veins, and passes upwards in the posterior interventricular groove to join the right end of the coronary sinus, either alone or in common with the right cardiac vein. It receives branches from the interventricular septum and from the posterior wall of both ventricles; but many of the veins from the left ventricle (**venæ ventriculi sinistri**, posterior cardiac veins) ascend on the posterior surface of the ventricle and open independently into the coronary sinus along its lower border.

D. The **right** (or small) **cardiac vein** is a slender branch which collects blood from the hinder parts of the right atrium and right ventricle. It runs transversely in the right part of the posterior coronary sulcus and opens into the right end of the coronary sinus, either independently or (as represents an earlier stage in development) in common with the posterior interventricular vein; occasionally (in 1 per cent. of hearts, [illegible]) it opens directly into the right atrium. Not

infrequently (in 20 per cent. of instances, PIQUAND) the right cardiac vein is much larger in size and is then joined by a number of veins which ascend on the anterior surface of the right ventricle and along the margo acutus, **vena marginalis dextra**; but more commonly these veins open independently into the right atrium. (See "Venæ Parvæ Cordis.") The right cardiac vein may lie above the coronary sulcus on the wall of the atrium.

E. The **oblique vein** of Marshall (vena obliqua atrii sinistræ) is a small straight vein which runs obliquely downwards on the posterior surface of the left atrium from below the left pulmonary veins and opens into the left extremity of the coronary sinus.

The **oblique vein**, especially in its upper part, is often impervious and in the form of a fibrous strand which may be traced upwards in front of the root of the left lung into a fold of the peri-

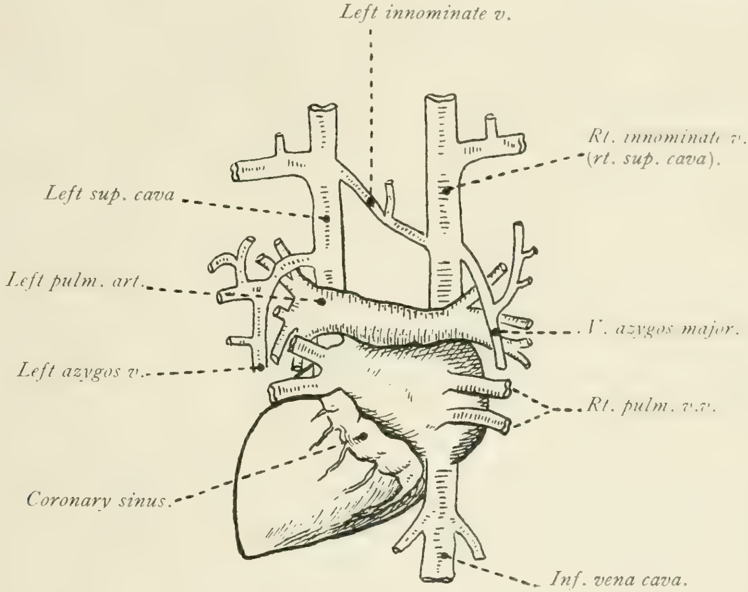


FIG 72.—A DIAGRAM OF THE HEART AND GREAT VEINS, FROM BEHIND, SHOWING THE ARRANGEMENT IN A CASE OF PERSISTENCE OF THE LEFT SUPERIOR CAVA.

cardium (vestigial fold of Marshall), and through it to the left superior intercostal vein as it crosses the arch of the aorta. Its opening in the coronary sinus is not provided with a valve. The coronary sinus and the oblique vein represent the persistent terminal parts of a typical left superior vena cava (duct of Cuvier with the left horn of the sinus venosus) and may be so developed. A considerable number of instances are recorded in which the left innominate vein, having been formed in the usual manner, does not cross the middle line to join the innominate vein of the right side, but is continued down in front of the arch of the aorta and in front of the root of the left lung to the heart, where it receives the left cardiac vein and then inclines to the right in the usual position of the coronary sinus and opens into the right atrium, thus giving rise to what has been termed a persistent left superior vena cava (fig. 72). This condition is normal in many animals, and its occurrence in the human subject is due, as is fully explained in the description of the mode of development of the great veins in Vol. I., to the persistence of the left anterior cardinal vein and left duct of Cuvier of the embryo. The fibrous cord mentioned above represents these parts, and if the opening of the coronary sinus into the right atrium be blocked (instances are quoted by HUTTON, *Jour. Anat.*, vol. xlix.; HARRIS, *Anat. Record*, vol. xxxvi.; GRUBER, *Virch. Arch.*, Bd. xcix.) the blood from the heart veins is conducted to the left innominate vein by the oblique vein and its upward continuations. In two instances the coronary sinus has been observed opening into the left atrium (LINDNER, JEFFREY); this abnormal termination must

be the result either of a malposition of the atrial septum or a secondarily acquired orifice which has not yet been explained.

The left marginal vein may run backwards above and separately from the left cardiac vein and open independently into the coronary sinus. The veins of the interventricular septum are large and anastomose freely with one another. Mention may be made of the **venæ telæ adiposæ**, which are specially abundant near the coronary sulcus; they join the superficial veins.

2. **Venæ Parvæ Cordis**.—The small veins of the heart form a series of which the main trunks lie on the surface of the heart and open directly into the right atrium (fig. 71). They consist of (*a*) three or four small veins which drain the anterior surface of the right ventricle, ascending on it parallel with one another and crossing the coronary sulcus; (*b*) the vein which ascends along the margo acutus (the vein of Galen), but which may, as already stated, join the right cardiac vein; and (*c*) one or two small veins which ascend on the posterior surface of the right ventricle, but which more frequently join the right cardiac vein. There are also to be included in this series (1) a vein which arises on the conus arteriosus and runs to the right with the arterial arch at the junction of the conus and the pulmonary artery; it opens into the right atrium between the root of the pulmonary artery and the atrial appendix (CRUVEILHIER); and (2) a vein which drains the roots of the aorta and pulmonary artery and the overlying part of the right atrial appendix and which opens into the appendix (ZUCKERKANDL).

3. **Venæ Minimæ Cordis**.—The smallest veins of the heart (veins of Thebesius) are small venous channels which commence in the substance of the heart wall and open directly into the chambers of the heart; in the heart wall, as is explained in the account of their development (p. 109), they communicate with the general venous system. They are most numerous in the atria where their orifices (the foramina of Thebesius, at the most ·5 mm. in diameter) are readily seen; but there are also some which open into the ventricles.

The existence of the **veins of Thebesius** has often been denied, among others by HALLER, CRUVEILHIER, and LUSCHKA, who held the foramina of Thebesius to be merely blind diverticula of the endocardium. By various methods of injection, however (BOCHDALEK, HENLE, HYRTL, LANGER, and many others), the presence of the veins as blood channels has been shown, first in the atria and subsequently in the ventricles; recently, however, NUSSBAUM has denied their presence in the ventricles. They occur in greatest number in the right atrium and especially on the septal wall in the region of the annulus ovalis and near the Thebesian valve; in the left atrium they are not so numerous, but are larger. It is probable that the foramina of Lannelongue belong to this system. In the ventricles the foramina of Thebesius are most frequent at the bases of the papillary muscles, in the region of the conus and, according to LANGER, at the apex of the heart. They do not communicate with the larger vessels except by capillary anastomoses and drain only the subendocardial tissue and the adjacent musculature.

Comparative Anatomy and Development of the Coronary Arteries.

The presence of coronary arteries is associated with the development of a cortical myocardium. In fishes, where the myocardium is almost entirely trabecular (p. 5) and the blood circulates in intertrabecular spaces through the whole thickness of the heart wall, there is no coronary circulation. In Amphibia the musculature of the atria and the ventricle resembles that of the fish heart, and there is no coronary blood supply to these parts, though a ventricular vein is sometimes described. The musculature of the bulbus, however, is more condensed and is supplied with coronary vessels; these extend for a short distance on to the ventricle, but they do not penetrate its wall. In the reptiles the cortical myocardium forms a considerable part of the heart wall and there is a definite coronary circulation to it. The coronary vessels, arteries and veins

are usually arranged in two groups, a cephalic group and a caudal group: (1) the cephalic arteries, which are small, descend from their origin from some of the neck arteries along the bulbus cordis region on to the ventricle, and the small cephalic veins enter the jugular veins; (2) the caudal arteries, which arise from branches of the dorsal aorta and reach the heart along the cardiac ligaments, form the main blood supply of the heart. The large caudal veins leave the heart along the cardiac ligaments and enter the epigastric veins and the ducts of Cuvier. The inner trabecular part of the myocardium retains a Thebesian sinusoid (intertrabecular space) circulation; and between the two circulations, coronary and Thebesian, a free anastomosis is established. In mammals, with the disappearance of the cardiac ligaments, the cephalic arteries become the sole arterial supply and their origin is shifted nearer the base of the heart until they arise from the root of the aorta; and the veins, representing the caudal venous system, no longer pass beyond the heart, but enter the sinus venosus (coronary sinus) or the atria. The trabecular muscle of the mammalian heart is small in amount, but retains a Thebesian circulation.

The development of the blood supply of the mammalian heart has been studied by GRANT (*Heart*, vol. xiii., 1926) in the rabbit. The early trabecular musculature (see p. 58) is provided with a Thebesian intertrabecular circulation, large sinusoid spaces lined with endothelium being formed in the heart wall; and, as the cortical musculature is formed, capillary formations grow into it from these spaces. The cardiac veins, which appear before the arteries, commence as outgrowths of the endothelium of the coronary sinus and spread first along the coronary sulcus to the bulbus cordis and then along the interventricular grooves to the apex of the ventricle; and from these regions branches grow over the surface of the heart and, entering the myocardium, communicate with the myocardial capillary network and through it with the Thebesian spaces. Outgrowths also occur from the endothelium of the atria and become linked with the coronary veins; they may retain their atrial connection and form the venæ parvæ cordis or ultimately open into the coronary sinus through their anastomoses. The arteries appear as outgrowths of the base of the aorta. They pass at first to the bulbus cordis and then spread over the rest of the heart, uniting as they advance with the capillary network already formed in the developing myocardium. The Thebesian intertrabecular circulation is much reduced, but retains its connections with the coronary capillary system and persists as an integral part of the adult myocardial blood supply. (See "Venæ Minimæ Cordis," p. 108.)

The connection between the Thebesian and coronary circulations may explain the rare anomalies of the coronary arteries described in the human subject by BLAKEWAY (*Jour. Anat.*, vol. lii.), in the dog by SCHAUDER (*Anat. Anz.*, Bd. lviii.), and in the ox by REID (*Jour. Anat.*, vol. lvii.). In them the anterior interventricular branch of the left coronary artery arose from the left ventricle near its apex, and in the first case this vessel was the only connection of the aorta with the chambers of the heart and through it alone the whole systemic circulation was maintained. The facts of pathology would indicate that there probably are special conditions of the circulation in the lower part of the anterior wall of the left ventricle.

THE LYMPH VESSELS OF THE HEART

The **superficial lymph vessels** of the heart lie in the subepicardial fibrous tissue, forming there a close network, the main stems of which follow the course of the blood vessels; it is possible, therefore, to distinguish a right and a left lymphatic field which correspond, more or less, with the arterial fields. The vessels of the right ventricle are collected posteriorly in a main trunk which ascends with the posterior interventricular artery and runs anteriorly with the right coronary artery in the coronary sulcus, receiving in its course numerous vessels from the walls of the ventricle. On the front of the heart it ascends in the groove between the aorta and the pulmonary artery and after piercing the pericardium in front of the aortic arch ends in the cardiac lymph glands. The vessels of the left ventricle drain into trunks corresponding to the branches of the left coronary artery, a large left lymphatic vessel being formed by the union of what may be named the circumflex and the anterior interventricular trunks. This vessel ascends on the posterior surface of the pulmonary artery and after piercing the pericardium behind the aorta joins the cardiac glands in front of the bifurcation of the trachea. Lymph glands have been described on the course of the lymph vessels in the subepicardial fibrous tissue; TANDLER states that many such glands (1 mm. in diameter) are to be found on microscopic examination. A larger gland (lymphoglandula subepicardiaca preaortica, RAINER), connected with the right lymph vessel, has been described in the fatty tissue round the root of the aorta; TANASESCU describes it to occur only in 3 per cent. of hearts. A second gland (l. subepicardiaca juxtapulmonalis, RAINER), connected with the left lymph vessel, lies on the left side of the pulmonary artery; TANASESCU states that he found it in 9 per cent. of hearts.

The distribution of the lymph vessels in the **myocardium** is by no means satisfactorily known. A statement of some of the earlier views is given in Vol. II., Part I., p. 324, and as is indicated there the descriptions given by ALBRECHT and by BOCK seem to be the most complete. According to BOCK, whose description is adopted by BARTELS, the lymph capillaries closely follow the blood capillaries and are very numerous; while ALBRECHT, in a similar way, has described large interfascicular vessels and draining into them an intermuscular capillary network which lies round the individual muscle elements. EBERTH and BELAJEFF have stated that the lymphatics of the heart are particularly difficult to inject in the human subject.

The **subendocardial** network is dense and extremely fine-meshed. It is connected with the myocardial vessels. EBERTH and BELAJEFF state that there are no lymphatics in the chordæ tendineæ; that they are to be found only in those parts of the atrio-ventricular valves in which muscle fibres and blood vessels are present; and that they are absent in the arterial valves. AAGAARD, however, in his recent extensive research, while able to demonstrate lymph vessels in the atrio-ventricular valves of the animal heart, was unable to discover them in the human heart. Care must be taken to distinguish between injected lymphatics and injections of the connecting system (AAGAARD).

THE NERVES OF THE HEART

The nerves of the heart are derived from the cervical sympathetic cords and the vagus nerves.[1] They arise some distance from the heart and have a considerable course in the neck and thorax before they reach it; close to the heart they unite to form the cardiac plexus from which leashes of fibres proceed to their distribution in the heart wall.

The **sympathetic cardiac nerves** are usually three in number on each side—superior, middle, and inferior, one arising, usually by more than one root, from each cervical ganglion and from the sympathetic cord adjacent to it. As they pass downwards in the neck the three trunks are connected with one another, with the upper cardiac branches of the vagus, and with the superior and inferior laryngeal nerves; and small ganglia[2] may sometimes be found on them, for example, the ganglion cardiacum superius on the superior trunk immediately caudal to the inferior thyreoid artery, and the ganglion cardiacum inferius of Wrisburg on the left superior trunk close to its entrance into the cardiac plexus. There are great individual differences in the number, size, and arrangement of the sympathetic trunks; they are often blended with one another, the right superior trunk is sometimes absent, or there may be a fourth nerve from the first thoracic ganglion. (For a fuller description of the course, relations, and variations of these nerves, see Vol. III., Part II., pp. 155-158; and v. SCHUMACHER, *Anat. Anz.*, Bd. xxi., and *Sitzungsber. d. k. k. Akad. d. Wiss. Wien.*, 1902; PERMAN; and GASKELL.)

The (parasympathetic) **cardiac branches** of the **vagus nerve** arise from it both in the neck and in the thorax. The upper cervical nerves arise in part from the main trunk and in part from the external laryngeal nerve, while others arise below this level. The thoracic branches, especially on the left side, arise very largely from the inferior laryngeal nerve; there are some cardiac nerves given off below the origin of the inferior laryngeal nerve, but at least several of them are distributed to the pericardium. In their course to the heart the vagal cardiac nerves are freely connected with the sympathetic cardiac nerves. (For details of the origin and course of these nerves, see Vol. III., Part II., p. 44.)

VESALIUS knew only of the left vagal thoracic branch to the heart, but a very full description of the cardiac nerves was founded by the classical researches of FALLOPIUS, who discovered all the cardiac nerves, with the exception of the right superior sympathetic branch, and described the connections they have with one another. The work of FALLOPIUS was completed by WILLIS, VIEUSSENS, WINSLOW, and others, and in 1794 SCARPA published his "Tables of the Cardiac Nerves," which contain an almost exhaustive statement. In the work of REMAK (1844) the ganglia of the heart were described for the first time, and since then the study of the nerve supply of the heart has been concerned with them, with the attempt to determine the distribution of the several nerves, and with the nature of the ultimate endings of the cardiac nerves in the cardiac muscle. (For further literature, see Vol. II., Part I., and Vol. III., Part II.)

The qualities of the nerve fibres which pass towards the heart in man are presumed to resemble in general those which have been determined by experiment in lower forms. In them it has been shown that the cardiac nerves contain both efferent and afferent fibres.

---

[1] Branches from the hypoglossal nerve may occasionally be traced to the cardiac nerves, but these are probably aberrant vagal fibres. The vagal fibres include those of the accessory nerve.

[2] The nature of these ganglia is as yet undecided; it is difficult to account for them if the cell stations of all the sympathetic fibres are in the inferior cervical and first thoracic ganglia (see p. 115).

The **sympathetic fibres** form an **accelerator** or **augmentor** series, for stimulation of them produces an increase in the frequency of the heart (which in the dog may be as much as 50 per cent.), an increase in the force of contraction of the atria and ventricles, and a shortening of the atrio-ventricular interval; they exercise only a slight tonic influence on the mammalian heart. The cell stations of these nerves are situated in the inferior cervical and first thoracic ganglia (or the stellate ganglion of some forms), and the connector (pre-ganglionic) fibres pass to these ganglia through the rami communicantes of the second and third, and to a small extent of the first and fourth, thoracic nerves.

The **vagal fibres** include some which when stimulated produce slowing (or arrest) of the heart, diminution of the force of contraction, and lengthening of the atrio-ventricular interval; the action is much weaker on the ventricles than on the atria.[1] These fibres form an **inhibitory** series. They exercise a considerable tonic influence on the heart, for after section of them there is an acceleration of the pulse rate. The degree of this vagal control varies greatly in different mammals, yet it may be stated (1) that animals with small hearts in proportion to the body weight (ratio less than ·4, see p. 120) have rapid pulses for their size when at rest, and section of the vagus causes little acceleration; and (2) that animals with large hearts (ratio more than ·6) have slow pulses for their size when at rest, and section of the vagus causes great acceleration. (See CLARK for examples.) In man vagal control is greatest in early adult life and least at the extremes of life. There are also included in the vagal fibres some which, when centripetally stimulated, produce a fall in blood pressure and a decrease in the force of contraction and in the rate of the heart beat; they form a **depressor** series and obviously act as the sensory part of a vagal (parasympathetic) reflex arc from the heart. The depressor nerve, or the nerve of CYON, is a distinct structure in the rabbit, being attached by two roots to the vagus, one (which is inconstant) to the main trunk, and the other (which is more constant) to the superior laryngeal nerve; in other mammals it is a much less independent structure, its fibres being included in the other cardiac nerves. In man it is usually held entirely to lose its individuality and to be incorporated in the sympathetic trunks, but VITI believes it to be represented by a branch of the superior laryngeal nerve which runs directly or indirectly to the cardiac plexus; this branch was present, he states, in 156 out of 200 dissections. It is sometimes named, in human anatomy, the nerve of HOFER. The path of these afferent fibres, which is a matter of importance in the operative treatment of angina pectoris, is thus not yet finally established; it is thought that they are scattered in the vagal and sympathetic cardiac nerves (and possibly in the vertebral sympathetic plexus), but it is also possible there may be a separate nerve, exclusively depressor, the nerve of HOFER.

A second group of sensory fibres consists of a series which pass in the rami communicantes and reach the posterior root ganglia of the last cervical and upper four thoracic nerves; they either end here or pass into the spinal cord, and are associated with the cutaneous sensory system. They form the sensory part of a sympathetic reflex arc, and constitute what is named a **pressor** series. Both the depressor and the pressor series, apparently, can conduct stimuli giving rise to sensations of pain. (The literature of the operative treatment of angina pectoris should be consulted for further details of the afferent nerves.)

The **cardiac plexus** receives the sympathetic and vagal cardiac nerves. It

[1] This holds in all vertebrates except a few reptiles; and, when it is possible to demonstrate it, the most powerful action of the vagus is in all forms on the sinus.

is a close network formation, so that it is a matter of difficulty to follow the individual cardiac nerves through the plexus to their distribution, though SCHUMACHER claims to have followed the right sympathetic branches to the right ventricle and those of the left sympathetic to the left ventricle; a similar bilateral distribution has been inferred from experimental work and from the distribution of pain in heart disease. Two parts of the cardiac plexus are distinguished, a superficial and a deep, but they are closely connected with one another, and the cardiac nerves which as a rule enter one of them may sometimes enter the other. The **superficial** cardiac plexus lies in the concavity of the arch of the aorta between the ligamentum arteriosum and the right pulmonary artery and superficial to the pericardium. In it there terminate, in whole or in part, two nerves of the left side, the superior sympathetic cardiac nerve and the lower cervical cardiac branch of the vagus nerve. The **deep** plexus, much larger than the superficial one, lies between the aorta and the bifurcation of the trachea. It consists of two lateral parts which are freely joined by numerous branches. It receives the great majority of the cardiac nerves, the exceptions being the two left nerves which enter the superficial plexus. (For further details of the cardiac plexus, see Vol. III., Part II., p. 164.)

The nerves which arise from the cardiac plexus proceed to the lungs (pulmonary plexuses, see Vol. III., Part II.) and to the heart. The cardiac branches are small and contain many fine non-medullated fibres. They descend to the heart in leashes along the aorta, pulmonary artery, and superior vena cava, and, according to PERMAN, may be arranged (in the human subject) in two groups, namely (1) those passing ventral to the transverse pericardial sinus and supplying the ventral surface of the heart, and (2) those passing dorsal to the transverse sinus and reaching the atria and thereafter the greater part of the dorsal surface of the ventricles. On both groups of fibres when they reach the heart wall, and especially on the posterior group, there are large numbers of ganglia interpolated on the nerve trunks; so that there are formed a large **atrial plexus** on the back of the atria, and an anterior plexus, smaller in its extent, which is distributed in the form of **coronary plexuses** along the coronary arteries to the ventricles. The right coronary plexus is derived from the superficial cardiac plexus and from the right part of the deep plexus, and the left coronary plexus, larger than the right, mainly from the left part of the deep cardiac plexus; and both receive considerable accessions from the atrial plexus.

The Ganglia of the Heart.—A ganglion in the ventricular septum of the calf was described by REMAK in 1844. The distribution of the ganglia in the heart of the frog was subsequently studied in great detail by REMAK, LUDWIG, BIDDER, and RANVIER. They showed that the two cardiac nerves unite on the posterior wall of the pulmonary vein in a plexus containing ganglionic masses (ganglion of REMAK). The nerves emerge from this plexus as the anterior and posterior nerves of the atrial septum; these run separately in the septum and have on them ganglionic masses which collectively form the ganglion of LUDWIG. At the lower end of the septum the two nerves unite again in a gangliated plexus, the ganglia being known as the ganglion of BIDDER. Below this there are separate branches passing to all parts of the ventricle, and as was shown by DOGIEL, ganglion cells are present on them throughout their course and even at the apex of the heart. The same wide distribution of ganglia is found in other Amphibia and in the Reptilia. The distribution of the ganglia in the Mammalia has been very variously described. All authors are agreed, however, that they are to be found throughout the atrial plexus, and in specially large numbers on the posterior wall of the left atrium, in the sulcus terminalis,

and in the atrial septum, and that they are to be found, though only at certain places, in the superficial myocardium as well as in the subepicardial tissue; and many specialised collections of them have been described, especially round the orifices of the great veins, in several forms. The earlier descriptions of the ventricular ganglia stated that they were to be found along the course of the nerves as far as the apex of the heart (VALEDINSKY, SMIRNOW, and MOLLARD), but most authors now restrict their distribution to the upper third of the ventricles (JACQUES, DOGIEL, VIGNAL), while SCHKLAREWSKY, FAHR, and PERMAN limit them to the upper parts of the interventricular furrows; an even more restricted distribution is described by EIGER, LISSAUER, and WOOLLARD, who hold that there are no ganglia on the ventricles, either subepicardially or in the myocardium, the atrio-ventricular sulcus forming their distal limit. The myocardial ganglion cells, previously described by several authors, are held by LISSAUER to be connective-tissue cells (mast cells of EHRLICH). DOGIEL and TUDOR JONES have described peculiar star-shaped cells in the ventricular subepicardium; DOGIEL holds them to be specialised connective tissue supporting cells of the sensory end-plates of the epicardium. Ganglia have been described in the upper part of the ventricular septum (JACQUES, LISSAUER), and large multipolar ganglion cells have been shown to be present in the atrio-ventricular bundle (WILSON).

It would thus appear from the numerous studies which have now been made that the details of the distribution and of the concentration of the cardiac ganglia vary with the species, and that they are smallest and most numerous in the human heart. It would also appear, however, that an arrangement in three groups may be defined: (1) A right group (sino-atrial ganglion, ASCHOFF), which lies round the orifice of the superior cava and in close relation with the sino-atrial node, into which it sends numerous fibres. (2) A left group (atrio-ventricular ganglion, ASCHOFF), much larger and more scattered than the right group, which lies on the dorsal wall of the atria in the neighbourhood of the atrial septum, extending to the left and perhaps reaching the left coronary veins, to the right and perhaps concentrated round the inferior cava, downwards to the coronary sulcus and specially gathered near the orifice of the coronary sinus, and in some forms extending forwards into the septum. Large strands of fibres, many of them having nerve cells on them, pass from the ganglia to the atrio-ventricular node and to the bundle of His. (3) A smaller group (ganglion of the bulbus, ASCHOFF) which lies on the anterior face of the left atrium and round the roots of the pulmonary artery and aorta; it extends on to the proximal part of the anterior wall of the ventricles (PERMAN).

It has been shown by HIS (junr.) that the bulbar and ventricular portions of the heart are supplied by the upper cardiac nerves and the atrial parts by nerves arising at a lower level. The earliest cardiac nerves to be developed are branches to the bulbus cordis from the vagus and sympathetic of both sides; they appear about the beginning of the fifth week and form a **bulbar plexus** between the aorta and the pulmonary trunk. In the seventh week they pass to the back of the atria and form there an **atrial plexus**, which receives sympathetic branches from the intermediate plexus (see below). The bulbar and atrial plexuses are connected by branches which are joined by offsets of both vagus nerves, the left recurrent nerve, and both sympathetic cords the whole constituting the **intermediate plexus**. Numerous ganglion cells of sympathetic nature (HIS) are found on all the plexuses. The coronary plexuses develop from the bulbar plexus and branches from the atrial plexus spread over the atria during the third month. The bulbar plexus, in the definitive condition, is thus

represented by the superficial and part of the deep cardiac plexus, and their anterior offsets with their coronary branches; the intermediate plexus is represented by the remainder of the deep cardiac plexus, and the atrial plexus by the network on the atria.

The **cardiac ganglia**, as thus described by HIS, would require to be considered to be of two kinds, sympathetic and parasympathetic, and to be the ending places of sympathetic and vagal (parasympathetic) nerve fibres. This conception of their dual nature is still largely held, and descriptions of specific differences have been given by MOLLARD, DOGIEL, MÜLLER, and others. It seems, however, to have been proved by experimental investigation that the cardiac ganglia belong exclusively to the vagal (parasympathetic) system, and the recent study by WOOLLARD would confirm this on a morphological basis; the factors which underlie the structural differences, which undoubtedly exist, are still to be determined. The matter requires fuller investigation, but it would also appear that the right and left groups of ganglia, which are related to the sino-atrial and atrio-ventricular nodes respectively, are the terminal ganglia of the right and left vagus nerves; the experimental evidence (COHN, GAUTER, ZAHN) seems to establish that the right vagus acts chiefly on the atria and the left vagus on the ventricles (see p. 96). The fibres which are distributed to the atria and to the connecting system would thus be derived from both the sympathetic and parasympathetic nerves, while the ventricular muscle, it would appear, is supplied only by sympathetic nerves.[1]

The **atrial plexus** and the **coronary plexuses** lie immediately beneath the epicardium. The atrial plexus is in the form of a network, while the coronary plexuses are distributed with the coronary arteries over the surface of the ventricles.[2] Numerous branches arise from the subepicardial plexuses. The smaller of these are distributed to the epicardium and to the superficial parts of the myocardium, while larger branches pass more deeply into the myocardium and end by supplying its middle parts and by forming a subendocardial plexus from which branches pass to the inner parts of the myocardium and to the endocardium. Three planes of the myocardium are thus distinguished (JACQUES), an external and an internal, innervated from the epicardial and endocardial plexuses, and a middle plane to which the fibres pass directly from the epicardial plexus. The motor nerve fibres, which are non-medullated, have been described by GERLACH to form in the frog three networks in the muscle substance, and the same description has been given by FISCHER for mammals. There is first a "ground" plexus made up of thick strands among the muscle bundles; from this branches arise which form a network round each bundle; and from this network there are given off the terminal branches which surround and end on the individual cells in a slight enlargement or varicosity which is applied to the surface of the cell or penetrates within the substance of the cell (intra-muscular plexus of GERLACH and RANVIER). There is, however, still considerable difference of opinion regarding the form of the motor endings; but the majority of recent writers (BOEKE, PERMAN, WOOLLARD, FUKUTAKE, MARCUS, JONES) describe the

---

[1] There is great difficulty in a morphological investigation of the distribution of the vagal and sympathetic systems in the heart; it is not only very difficult to distinguish the post-ganglionic fibres of the cardiac ganglia from other post-ganglionic fibres, but also, according to MÜLLER, at least 70 per cent. of the pre-ganglionic fibres of the vagus are non-medullated.

[2] These nerves are not easily dissected in the human heart, but in other forms (dog, cat, calf) large branches, easily seen without dissection, are directed towards the apex of the heart; they run more or less parallel with one another and independently of the branches of the coronary arteries.

nerve fibrils as passing into the substance of the muscle cells and there ending in a variety of forms, in the interpretation of which the whole question of the relation of nerve and muscle is involved. (It is a significant fact in this respect that intra-muscular nerve endings have not been described in the connecting systems.) In fishes, amphibians, and reptiles, the nerve endings are said to be distributed over the greater part of the cell, while in mammals the final branch is restricted to a comparatively small part of it near the nucleus (SMIRNOW).

Sensory nerve-endings have been described in all the layers of the heart wall. In the epicardium and endocardium their number is extraordinarily great, and specialised end plates have been described in both layers. (See Vol. II., Part I.; WOOLLARD; JONES; BOEKE.) In the myocardium there are numerous nerve endings of less definite form in the connective tissue which are believed to be sensory structures.

Chromaffin tissue is said to occur in the coronary sulcus. WIESEL ("Die Erkrankungen arterieller Gefässe im Verlange akuter Infectionen," *Zeitsch. f. Heilkunde*, 1907) has described a small chromaffin body, 3 or 4 mm. long, close to the origin of the left coronary artery; he states that it is to be found more often in the young, and that in children other small nests of chromaffin cells are to be discovered in the coronary sulcus.

POSITION OF THE HEART

The **heart** is situated in the thorax, forming there the chief part of the median thoracic septum, the mediastinum, which extends from the vertebral column behind to the sternum in front and separates the two pleural chambers. The heart lies, therefore, between the lungs. It is nearer to the front than the back of the chest, but for the most part is separated from the anterior thoracic wall by the pleuræ and the thin anterior margins of the lungs (fig. 73). It is enveloped, with the adjacent parts of the two aortæ and the great veins, by a membranous covering, the **pericardium**, which intervenes between it and the neighbouring structures.

The base of the heart lies opposite the fifth, sixth, seventh, and eighth thoracic vertebræ, from which it is separated by the pericardium and the œsophagus and descending aorta. The diaphragmatic surface rests on the diaphragm. The anterior (sterno-costal) surface may be depicted on the anterior surface of the thorax in relation to the sternum and the costal cartilages, the area of the chest wall so related to the heart being named the precordial region.

The greater part, fully two thirds, of the bulk of the heart lies to the left of the median plane (fig. 73). The right atrium lies behind the sternal ends of the third, fourth, fifth, and sixth right costal cartilages and the intervening portions of the intercostal spaces, and is also partly covered by the right edge of the sternum; and the right margin of the heart, which it forms, is represented by a curved line from the upper edge of the third costal cartilage, a quarter to half an inch from the border of the sternum, to the lower border of the sixth costal cartilage three quarters of an inch from the border of the sternum, the greatest convexity of the curve being in the fourth intercostal space and one inch from the border of the sternum. The point of the right auricular appendage is behind, or even slightly to the left of, the middle line on a level with the third costal cartilage. The left atrium extends vertically from the lower border of the second left costal cartilage to the upper border of the fourth cartilage, its left margin

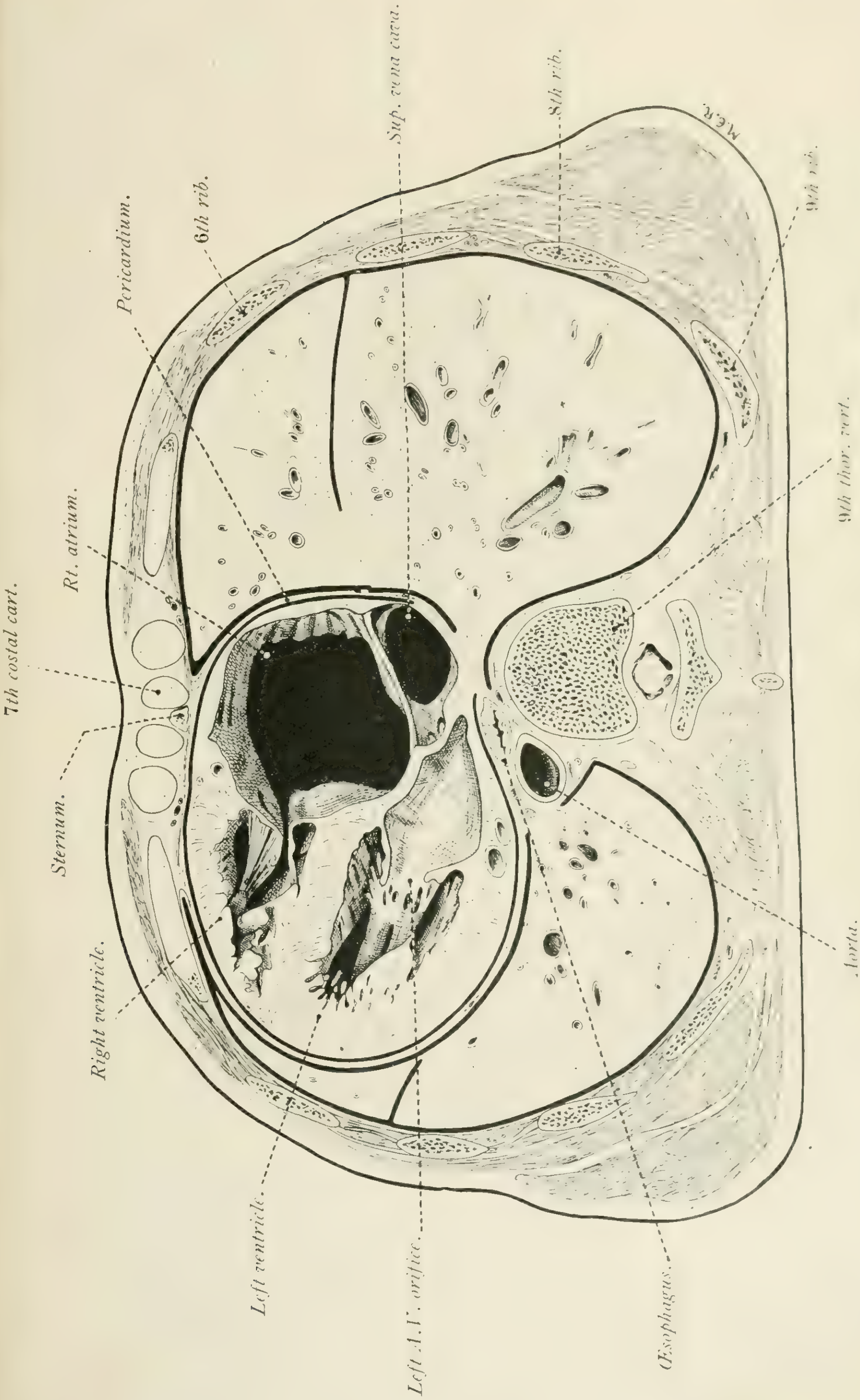


FIG. 73.—TRANSVERSE SECTION OF THE THORAX OF A MAN. ÆT. FIFTY YEARS.

The section passes through the ninth thoracic vertebra behind and the tips of the seventh costal cartilages in front.

forming the upper part of the left border of the heart. The apex of its auricular appendage is behind the third costal cartilage, about an inch and a quarter to the left of the margin of the sternum. The right ventricle lies behind the sternum and the third to the sixth cartilages of the left side. Its middle and lower part is, as a rule, the only part of the heart uncovered by the lungs, and this area, the area of absolute dullness, may be marked off by two lines drawn from the position of the apex beat to the middle line of the sternum, one line running horizontally and the other extending obliquely upwards to between the fourth

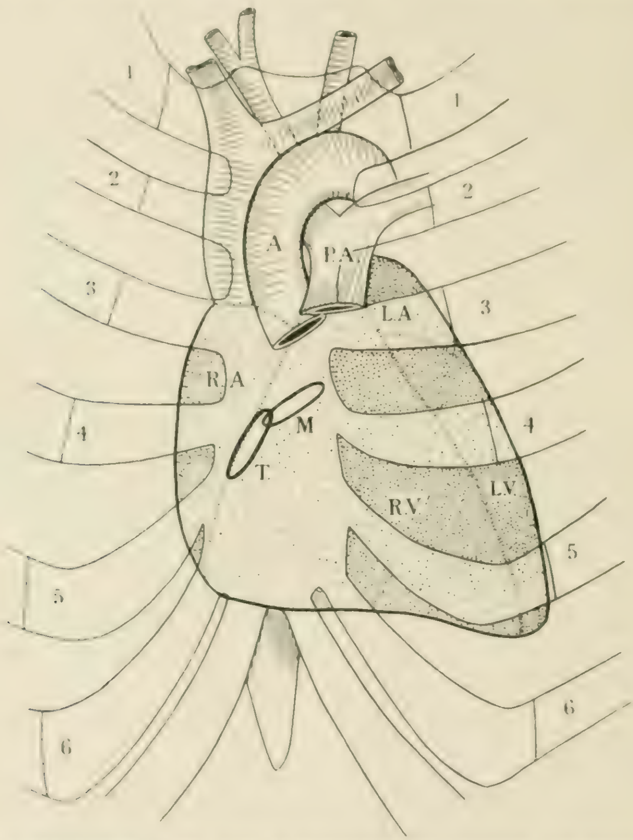


FIG. 74.—A DIAGRAM TO SHOW THE RELATIONS OF THE HEART AND GREAT VESSELS TO THE SKELETON OF THE ANTERIOR WALL OF THE THORAX.
M, mitral orifice ; T, tricuspid orifice.

costal cartilages; but sometimes, especially during expiration, a small portion of the left ventricle near the apex is also exposed. The lower border of the heart (margo acutus), which is formed chiefly by the right ventricle, passes from the sternal end of the sixth cartilage on the right nearly transversely behind the seventh right cartilage, the sterno-xiphoid junction, and the seventh and sixth left cartilages, to meet the left margin at the apex of the heart in the fifth space; the line thus drawn should be slightly convex upwards. The left ventricle forms a narrow strip along the left margin (margo obtusus) of the heart. This margin, curved convexly to the left, extends from the apex of the heart in the fifth space to the third space an inch from the left border of the sternum (ventricular part), and above this to the lower border of the second cartilage half an inch from the border of

the sternum (atrial part). The apex of the heart is situated in the fifth left intercostal space three and one-half to four inches from the middle line, and just within a line drawn vertically downwards from the nipple; the nipple, however, varies so much in its position that the relation between the apex of the heart and the nipple line is not constant. The position of the apex beat, the point of maximum impulse of the heart on the chest wall, does not coincide with the apex of the heart; it lies about half an inch medial to it in the fifth interspace.

The coronary (atrio-ventricular) sulcus corresponds with a line drawn obliquely downwards from the sternal end of the third left cartilage to the sternal end of the sixth right cartilage (fig. 73). The atrio-ventricular openings lie parallel with and slightly below the line of the coronary sulcus. The right (tricuspid) orifice lies behind the middle of the sternum on a level with the fourth intercostal space and the fifth cartilage, and the left (mitral) orifice, not so obliquely placed, lies behind the left part of the sternum opposite the fourth left costal cartilage. The orifice of the pulmonary artery is placed immediately to the left of the sternum at the upper edge of the third cartilage and the pulmonary trunk extends up to the second cartilage. The aortic orifice is behind the left half of the sternum on a level with the lower border of the third cartilage; it is a little below and to the right of the pulmonary orifice, by which it is covered to the extent of one-fourth of its diameter, and it lies exactly behind the upper part of the infundibulum of the right ventricle. The aorta passes upwards and to the right behind the sternum to the medial end of the second right costal cartilage.

The position of the heart varies individually. In children the heart is relatively broader and projects more to the left side of the chest than in the adult, so that the apex beat is often to be felt in, or even lateral to, the nipple line; in old persons the heart frequently occupies a much lower position than that described above. The position is also influenced, though only slightly, by the respiratory movements and by the posture of the body; in inspiration, when the diaphragm sinks and the lungs expand, the heart recedes slightly from the chest wall; and it comes more into contact with the anterior wall when the body is in the prone position or is lying on the left side. X-ray examination has shown that the base of the heart and roots of the lungs are moved downwards and forwards in inspiration so that the base of the heart is separated by a greater distance from the vertebral column. In the dead the heart is a little higher in position than in the living.

DIMENSIONS OF THE HEART

The various dimensions of the adult heart are matters of clinical and pathological importance, and they are not without some theoretical interest. All of them, it will be noted from the figures which are given, show considerable ranges of variation, but while there are certain modifying factors, it may be said that in general the dimensions of the heart are related to the weight of the body and to the musculature of the individual. There are necessarily, therefore, considerable differences in the sexes, the heart being smaller in all its dimensions in the female, and, of course, there are great differences at different ages.

Weight of the Heart.—The weight of the healthy adult heart (the aorta and the pulmonary artery having been cut across close to the heart and the heart having been opened and washed) is in the male on an average 11 to 12 oz. (310 to 340 gms.), the range, however, being from 9 to 15 oz. (255 to 420 gms.), and in the female 10 to 11 oz. (280 to 320 gms.), the range being from 7 to 14 oz. (200 to 400 gms.). The following figures have also been given (Table); there are many others, ranging within wide limits (see TANDLER), but often the technique of the measurement is not indicated and it is doubtful how far the figures can be compared.

WEIGHT OF THE HEART

	Male.	Female.
BOLLINGER	340 gms.	275 gms.
JUNKER	348 „	269 „
[illegible]	340 „	273 „
KALMANSOHN	332 „	264 „
BLOSSFELD	346 „	310 „

The weight of the heart in the adult (male and female) is thus on an average 310 gms., but it varies from 200 to 420 gms. (210 to 450 gms., HENLE). It has long been known, in the study of this wide range of size, that greater body weight is associated with greater heart weight, that is, that the weight of the heart increases with the body weight; but, it is also known, the increase is in a diminishing ratio, so that with a higher body weight the proportional weight of the heart is lower. This is clearly shown in the following table (from CLARK, where further references are to be found; see also JOSEPH, *Jour. Exp. Med.*, vol. x., where a list of the important papers is to be found).

HEART RATIOS

	Small Animals.		Large Animals.	
	Body Weight.	Heart Ratio.	Body Weight.	Heart Ratio.
Frankonian sheep . .	45·9 kil.	·464	53·4 kil.	·420
Southdown sheep . .	37·0 „	·452	46·8 „	·429
Oxen	659·0 „	·424	838·0 „	·387
Bulls	478·0 „	·485	829·0 „	·364
Cows	445·0 „	·509	530·0 „	·468
Men	47·0 „	·613	68·0 „	·535
Dogs	4·13 „	·943	15·3 „	·685

$$\text{Heart ratio} = \frac{\text{Heart weight}}{\text{Body weight}} \times 100.$$

The heart ratios in man expressed in this table are ·613 and ·535, that is, the proportion of heart weight to body weight is 1 : 163 and 1 : 187; many other figures have been given, the extremes of which are the proportions of 1 : 150 (WEBER) and 1 : 240 (ROBINSON), representing ratios of ·66 and ·42. In most of the published results the individual measurements are not given, but the figures in the table above suggest that in man (and in the ox, bull, and cow) the heart weight varies as (body weight)$^{0\cdot 6}$, while in the sheep and dog, on the other hand, the heart weight varies as (body weight)$^{0\cdot 8}$ The figures for several other species (mice, rats, rabbits) and for the human during the early years of life also suggest that (when the comparison is made between animals of the same species but of different weights) the heart weight varies as (body weight)$^{0\cdot 8}$. It is probable that in man (and in cattle), in which the heart weight increases only as (body weight)$^{0\cdot 6}$, that the extra body weight in the heavier individuals is largely fat; and that, therefore, as was long ago suggested, the musculature of the individual is, for heart size, the important element of the body

weight. This fact is established by an examination of the heart ratios of animals of different modes of life (Table, from CLARK), for it is then clearly shown that those animals which are capable of severe and continued muscular work have much higher ratios than those animals which depend for their safety upon holes or other inactive means.

HEART RATIOS IN ANIMALS

Deer	1·15	Guinea-pig	·42
Wolf	1·01	Norwegian rat	·4
Fox	·92	Wild boar	·39
Seal	·92	Hedgehog	·38
Hare	·77	Rabbit	·3

It has also been shown that in the same species animals distinguished for muscular work have larger hearts than less active animals; thoroughbred race-horses and greyhounds have larger heart ratios than ordinary horses and dogs (HESSE, *Zool. Jahrb. Abt. Allg. Zool.*, 38, 1921), and the hearts of wild animals are larger than those of confined animals (ROBINSON, 1748). There is still some dispute as to whether enlargement of the heart can be induced in the individual by muscular exercise, but experimental work in animals (see CLARK for references) and X-ray examinations in man strongly support the view that an increase can be induced; in man the increase is most evident in long-distance runners, cyclists, and swimmers (BARDEEN, "Determination of the Size of the Heart by X-rays," *Amer. Jour. Anat.*, vol. xxiii., 1918; DIETHLEN, "Moderne Methoden der Kreislaufs Diagnostik," 1925). It must be further added that from the observations of STROHL on alpine and moor ptarmigan, and of HESSE on squirrels from areas of different mean temperature, it appears that animals living at high altitudes or in cold climates have higher heart ratios than similar animals living at low altitudes or in warm climates.

At birth the heart weighs on an average $13\frac{1}{2}$ drachms (21 gms., MÜLLER; 23 to 24 gms., VIERORDT), and its proportion to the body weight is 1 : 120 (MECKEL), 1 : 130 (in the last edition of this work), and 1 : 132 (VIERORDT); on these figures the heart ratio is ·83, ·77, ·76. The difference between these figures and those for the adult (mean ratio, say, ·55) is not, therefore, very great; for the higher circulatory needs of the young (and of small animals generally) are principally met by the higher pulse rate. There is at first a definite decrease in the rate of growth of the heart, which is probably associated with the loss of the placental circulation, but thereafter the weight of the heart increases rapidly during the first years of life, closely following the curve of the increase of the body weight in the ratio of (body weight)$^{0\cdot8}$; it then grows more slowly until the approach of puberty when, with the great increase of the voluntary musculature, another period of more rapid growth sets in; this is shown in the following table :—

WEIGHT OF HEART (in grams)

	MÜLLER.	VIERORDT.	JUNCKER.
At birth	21	23 to 24	...
,, 1 year	32	33 ,, 41	36
,, 2 years	42	51	45
,, 4 ,,	62	69 to 74	64
,, 6 to 10 years	82 to 103	87 ,, 130	...
,, 11 ,, 14 ,,	119 ,, 126	125 ,, 173	...
,, 15 ,, 20 ,,	215 ,, 236	200 ,, 298	...

After adult age is reached the heart continues to increase in weight, according to MÜLLER, BIZOT, and GLENDINNING, until about 70 years of age; according to BENEKE it increases until 50 years, remains stationary until 70 years, and increases slightly afterwards; and according to THOMA it increases until 35 years, remains constant until 45 years, and thereafter increases until 65 years.

In states of experimental inanition in rats (JACKSON, *Amer. Jour. Anat.*, vol. xviii.) the heart loses weight in nearly the same proportion as the whole body; in conditions of wasting in man the heart loses weight in a smaller proportion than the body and, therefore, increases in relative weight (ASCHOFF, *Path. Anat.*, Bd. I).

The Volume of the Heart.—The volume of the heart was found by BENEKE to increase with age, at first rapidly and then gradually. Thus in the newborn infant the average volume is 22 c.c.; at the fifteenth year it is 150 to 160 c.c.; and at the twentieth year about 250 c.c. After this it increases but slowly up to the fiftieth year, at which time its volume is 280 c.c. (196 to 322 c.c., HENLE; 218 to 358 c.c., KRAUSE; 260 to 310 c.c., BENEKE); subsequent to this there is a gradual slight diminution. The volume is about the same in the two sexes up to the age of puberty, but after puberty it is 25 to 30 c.c. larger in the male. On account of the obvious difficulties of the investigation these several statements can only be regarded as approximate.

Measurements of the Heart. Linear measurements of a flaccid organ like the heart are subject to so many accidental variations that they are of little value, but it is generally considered to be about 5½ in. long in its greatest length, 3½ in. in its greatest width, and 3 in. in its extreme thickness from the sternal to the diaphragmatic surface. Very similar though slightly higher figures are given by CRUVEILHIER and HENLE, while according to HOFFMANN the limits of the normal measurements are as follows: greatest length, 125 to 150 mm.; greatest breadth, 90 to 130 mm.; and greatest thickness, 53 to 80 mm.

The Atrio-Ventricular Orifices.—The circumference of these orifices may be accurately measured by passing through them graduated wooden cones; their average dimensions are given below, the limits inserted being those within which the results of most writers fall.

CIRCUMFERENCE OF THE ATRIO-VENTRICULAR ORIFICES
(in mm.)

	Male.	Female.
Right orifice	122 (119 to 128)	115 (106 to 120)
Left orifice	103 (99 to 112)	100 (93 to 103)

The right orifice is thus larger than the left in the proportion 100 : 84 (100 : 80, LANDOLFI). At birth the right orifice measures 28·5 mm. and the left orifice 26·5 mm. (CREUTZFELDT). They vary together in size, and, as is shown in the following measurements of CREUTZFELDT, they definitely increase in size after fifty years of age.

CIRCUMFERENCE OF THE ATRIO-VENTRICULAR ORIFICES (in mm.)

	Right Orifice.		Left Orifice.	
	Male.	Female.	Male.	Female.
20 to 40 years . . .	123·5	111·0	109·1	96·2
40 ,, 50 ,, . . .	126·6	118·8	111·0	100·2
50 years . . .	131·7	122·0	115·0	103·2

It has already been pointed out that during life these orifices are not circular in shape, so that their diameter and surface area can be only relatively determined. On the figures given above the average diameters and areas are as follows:

	Diameter (in mm.).		Area (in sq. mm.).	
	Male.	Female.	Male.	Female.
Right orifice . . .	39	36	1,194	1,017
Left orifice . . .	32	31	855	804

The surface area of the cusps of the tricuspid valve has been given as 2,378 sq. mm. in the male and 2,001 sq. mm. in the female, and of the mitral valve as 1,868 sq. mm. in the male and 1,434 sq. mm. in the female (Creutzfeldt). The surface area of the atrio-ventricular valves is thus much greater than the area of the atrio-ventricular orifices, the proportion of the valve area to orifice area being on the right side 1 : 1·4 to 1 : 1·8, and on the left side 1 : 1·5 to 1 : 2·2.

The Arterial Orifices.—The following are the measurements of the arterial orifices; the higher figures of the circumference measurements are taken from Peacock's tables, and the other measurements are calculated from them.

MEASUREMENTS OF ARTERIAL ORIFICES

	Circumference (in mm.).		Area.		Diameter (in mm.).	
	Male.	Female.	Male.	Female.	Male.	Female.
Aorta . . .	70 to 81	64 to 76	530 sq.mm.	452 sq.mm.	26	24
Pulmonary artery .	72 ,, 91	66 ,, 89	660 ,,	615 ,,	29	28

The pulmonary orifice, all writers are agreed, is larger than the aortic orifice, in the proportion of 100 : 88·5 (Peacock); Buhl gives the proportion at the sinuses of Valsalva as 100 : 92·5, and Beneke the proportion of the arteries at 1 cm. above the margin of the valves as 100 : 98. At birth the pulmonary

artery measures 23·7 mm. and the aorta 18·1 mm. (BENEKE). The area of the cross section of the aorta has been shown to vary as (heart weight)$^{0.8}$; for measurements and references, see CLARK.

Dimensions of the Ventricles The average thickness of the walls of the right and left ventricles is shown in the following table :—

THICKNESS OF WALLS OF VENTRICLES (in mm.)

	PEACOCK.		BIZOT.	
	Right Ventricle.	Left Ventricle.	Right Ventricle.	Left Ventricle.
At base	2·8	11·0	4·1	10·2
Middle	4·2	12·8	3·1	10·9
Near apex	2·8	5·4	2·2	8·2

The muscular part of the septum is between 9 mm. and 12 mm. thick, and the pars membranacea septi about 1·5 mm. thick.

During the later months of fœtal life the muscular walls of the two ventricles are of equal bulk, but after birth the right wall grows much less than the left, so that at the end of the second year the left is twice the bulk of the right, a proportion which is thenceforward maintained; in the adult (of 50 to 70 kilos body weight) the weight of the left ventricle is 157·7 gms. and of the right ventricle 77·5 gms. (MÜLLER). The comparison of the weights of the right and left ventricles gives the **functional index** of the heart; on MÜLLER's figures (obtained by a method in which the interventricular septum is divided) this is ·508 in the male and ·506 in the female. Other methods of calculating this index are described by CLARK.

The Capacity of the Heart.—The capacity of the different chambers of the heart has been a matter of interest since classical times; ROBIN (*Jour. de l'Anat. et de la Phys.*, 1864), in an historical review of the subject, has given an account of the various conclusions which have been reached. There has been, it would appear, from early times almost a consensus of opinion that the right chambers of the heart are slightly more capacious than the left chambers; and certainly in the ordinary modes of death the right ventricle is always found more capacious than the left ventricle, containing much more blood-clot and being less fully contracted, and the right atrium is generally more capacious than the left atrium. It has been maintained, however, apparently in view of the fact that the volume output of the two sides of the heart must be the same over even a short period, that during life the capacity of the two sides of the heart cannot be different, and the difference which is found after death has been explained by supposing a regurgitation of blood from the lungs into the right ventricle, and in other ways. The measurements obtained by HIFFELSHEIM and ROBIN (by injecting the cavities with wax) are as follows :—

CAPACITY OF THE CHAMBERS OF THE HEART

Right atrium . .	100 to 185 c.c.	Left atrium . .	100 to 130 c.c.
Right ventricle . .	160 ,, 230 c.c.	Left ventricle .	143 ,, 212 c.c.

The capacity of the atria is here shown to be smaller than the capacity of the ventricles and the left chambers smaller than the right; the difference in the

capacity of the ventricles need not, of course, affect the volume of the output, for it is probable, as already suggested (p. 65), that the amount of blood remaining in the right ventricle at the end of systole is greater than the amount remaining in the left ventricle. The classical belief that some of the water of the blood is evaporated in the lungs to saturate the expired air, that the blood loses bulk in its passage through the lungs, and that therefore the left ventricle is necessarily smaller than the right, receives an interesting confirmation if it prove correct, as has been stated, that the specific gravity of the blood in the right ventricle is lower than that of the blood in the left ventricle (TERRY, *Anat. Record*, vol. xxxvi.). The presence of blood in the right ventricle after death is probably due to the fact that the right atrium is *ultimum moriens*.

The Heart in Pregnancy.—It was first enunciated by LARCHER (1828) that the heart is enlarged during pregnancy, the enlargement being chiefly of the left ventricle to meet the increased requirements of the mother and the needs of the fœtus, and that it returns to its normal size during lactation. The fact of this enlargement has been denied, but the consensus of opinion (DUCREST, ENGEL, BENEKE, DREYSEL, OLIVER) now is that there is a slight increase (about 6 per cent.) in the size and weight of the heart up to the time of parturition. (For tables of heart weights at different periods of pregnancy and lactation, see DREYSEL, *Münch. med. Abhand. Arb. a. d. path. Instit.*, 1 Reihe, H. 3, and TANDLER). It has also been shown by X-ray examination that the area of the superficial surface of the heart is increased during pregnancy. The increase is greater in younger than in older women. It has been determined that in pregnancy the ventricular systole is stronger and the contents of the heart are discharged under higher pressure (OLIVER, *Brit. Med. Jour.*, vol. i., 1927); if there is no hypertrophy then some other mechanism must be called into play. Many patients are thus conscious only during pregnancy of cardiac deficiency.

ABNORMALITIES OF THE HEART

Abnormalities in the conformation of the heart are common conditions. Many of them are slight departures from the normal and they give rise to no apparent disability, though it has been suggested that they shorten the duration of life; others are definitely associated with disability and early death. Some are of such gravity that though the heart may function during the early months of life it cannot meet the demands of the exertion of learning to walk, and death occurs in the first or second year; while others depart so greatly from the normal that they are inconsistent with an extra-uterine existence. Numerous instances of all the types of abnormality are recorded in anatomical and other literature, and there is a large index of them in the Catalogue of the Surgeon-General of the United States Army; more systematic accounts are given by PEACOCK, ROKITANSKY, THERÉMIN, KEITH, MÖNCKEBERG, SCHWALBE, and LAUBRY and PEZZI. It is proposed here only to summarise the more common defects and to omit both morphological and clinical discussions.

The early heart, it will be remembered (p. 16), consists of the following parts from the posterior to the anterior end—sinus venosus, atrium, atrial canal, ventricle, and bulbus cordis; and it assumes its definitive conformation, apart from its growth, as the result of two processes: (1) the incorporation of some of the chambers into others, and (2) the formation of septa in the chambers so that they are divided into right and left halves. The sinus venosus, as has been described, is absorbed

into the right atrium, the atrial canal is overgrown by the atrium and the ventricle, and the bulbus cordis is included in the right ventricle, while the formation of septa occurs in the atrium, atrial canal, ventricle, and bulbus cordis. The abnormalities of the heart are conveniently described as failures or defects of these two developmental processes, so that they may be classified as (1) failures or defects of the processes by which one part is incorporated with another, and (2) failures or defects in the formation of the septa.

1. **Failures or Defects in the Incorporation of the Sinus Venosus.** Failures of the incorporation of the sinus venosus into the right atrium are extremely uncommon, for the absorption occurs at an early period (fifth week) of development; and they are usually associated with other grave cardiac malformations incompatible with an extra-uterine life. Examples of this condition are described by ALLANDARY and PAPILLIAN. The sinus venosus in these cases persists as a separate chamber of the heart. It forms a small sac on the posterior surface of the atrium, and receives the inferior cava, the right and left superior cavæ, and independently the cardiac veins from the ventricles, the coronary sinus being represented by the terminal part of the left superior cava. The pulmonary veins, which are usually unabsorbed into the left atrium, may appear also to open into the sinus, but an examination of the interior demonstrates that the common pulmonary stem opens into the common atrium on the left side of the sino-atrial orifice. This orifice, oval in shape and rather vertical in position, is bounded at the sides by folds which represent the right and left venous valves. The atrial septum is represented by a rudiment of the septum primum. There is a single atrio-ventricular orifice. The ventricular and bulbar parts of the heart may be normal.

Remains of the venous valves, as has already been described (p. 32), are often to be found on the atrial septum. There are a few records of more complete persistence of the valves (KEITH); they bound an orifice between two parts of the right atrium, the posterior being the sinus part and receiving the venæ cavæ and the coronary sinus, and the anterior having opening out of it the right atrio-ventricular orifice.

2. **Failures or Defects in the Incorporation of the Pulmonary Veins in the Left Atrium.**—The vestibular part of the left atrium is formed by the expansion and absorption into the heart of the common stem and proximal parts of the pulmonary veins (pp. 13 and 41). This process may fail to occur and the four pulmonary veins then unite into a common stem which opens into the back part of the left atrium proper; KEITH describes three such cases. An incomplete absorption explains those cases in which an abnormal septum is present in the left atrium at the junction of the atrium proper and the vestibule and divides it into two parts, a posterior which receives the pulmonary veins and an anterior into which the appendix opens and in the floor of which there lies the atrio-ventricular orifice. (See POTTER and RANSON, *Jour. Anat.*, 1901.)

3. **Failure or Defects in the Incorporation of the Bulbus Cordis.** A large number, probably nearly 70 per cent., of the malformations of the heart are due to a failure or arrest of the incorporation of the bulbus cordis in the ventricular part of the heart. (On the details of the process of the incorporation of the bulbus, see p. 19, and especially KEITH, *Lancet*, vol. ii., 1909; and *ibid.*, vol. ii., 1921.) Several varieties of this defect may be recognised.

(a) There may be an almost complete arrest in the development of the bulbus cordis. The infundibular part of the right ventricle is then a mere slit, though the body of the ventricle is well developed. The orifice of the pulmonary artery is represented by a fibrous mass, which may be impervious or perforated by a

small opening, round which the rudiments of the pulmonary valve can be distinguished; and the pulmonary artery is absent at its commencement or is represented by a fibrous thread. An interventricular foramen is always present. The ductus arteriosus is patent in 30 per cent. of cases (KEITH); if it is occluded then the pulmonary circulation is maintained by the bronchial arteries and numerous accessory branches of the intercostal arteries which may be equal in size to the radial artery.

(*b*) The bulbus may be present but have undergone no expansion, thus producing a congenital pulmonary stenosis. The infundibular part of the right ventricle is here a small fusiform cavity, the opening of which into the body of the ventricle is constricted either by a fibrous ring or by a circular thickening of the endocardium. The pulmonary valves are often fused. An interventricular foramen is usually present.

A congenital pulmonary stenosis may be entirely due, however, to fusion of the pulmonary valves, there being no developmental arrest in the expansion or incorporation of the bulbus in the ventricle. The valves form an inverted cup-shaped diaphragm, perforated in the centre by a larger or smaller opening.

(*c*) The bulbus may be normally developed but imperfectly incorporated in the right ventricle. There is then a constricting muscular ring between the infundibular part and the body of the ventricle, the margin of the ring being fibrous tissue; and the orifice between the two parts may be as small as 4 mm. in diameter. The ring is, of course, but an exaggeration of the normal muscular ring between the inflowing and outflowing parts of the ventricle of which the moderator band and supraventricular crest form parts (p. 50). The infundibular part of the ventricle is usually dilated, and in the body there is nearly always an interventricular foramen.

(*d*) *Transposition of the Arterial Stems.*—In this rather uncommon malformation the pulmonary artery arises from the left ventricle and the aorta arises in front of it from the infundibulum of the right ventricle, that is, there is a transposition of the arterial stems to the opposite ventricle. (A recent case is described by HARRIS, *Anat. Record*, vol. xxxvi.) This condition, according to KEITH, is due to a reversal of the atrophic and expansion processes in the bulbus, the pulmonary part undergoing an abnormal atrophy and the aortic part an abnormal expansion. It is interesting to note in these cases that the septal cusps of the aortic valve are still the coronary cusps, and are therefore posterior in position. There is usually a stenosis of the pulmonary orifice. The right heart in these cases is, of course, entirely a systemic heart and the left heart a pulmonary heart, and if an extra-uterine life is to be possible the septa of the heart must be incomplete or/and there must be a free connection between the systemic and pulmonary veins; the interventricular septum is, therefore, undeveloped or there is a large interventricular foramen, and the foramen ovale is widely open or the atrial septum is incompletely formed. The ductus arteriosus is usually patent, and there is a very free communication between the pulmonary arteries and veins and the bronchial system (KEITH).

(*e*) *Aortic Stenosis.*—Congenital aortic stenosis, a fusion of the aortic cusps and constriction of the aortic orifice comparable to the pulmonary stenosis described above, is uncommon, but several cases are described by THERÉMIN. A condition of complete atresia of the aortic orifice, with a cord-like condition of the ascending aorta, has been described; it is associated with a small left ventricle, a patent ductus arteriosus, and a patent foramen ovale conducting from the left to the right atrium. (See BLAKE, *Jour. Anat.*, vol. xxxv.) A subaortic stenosis,

due to a constricting band of subendocardial fibrous tissue round the left ventricle just below the aortic orifice, is a recognised though very rare abnormality.

4. **Failures or Defects in the Formation of the Cardiac Septa.** (*a*) *The Atrial Septum.*—The formation of the atrial septum has been described (p. 37), and three foramina which may be present in it, representing defects in its completion, have also been described; these foramina are the foramen ovale, the foramen primum, and a foramen above and behind the foramen ovale, the presence of which it is difficult to explain. The atrial septum, however, may be entirely or almost entirely absent, there being then a common atrial chamber in which the rudiment of the septum primum, projecting as a ridge from the posterior wall and adjacent parts of the roof and floor, may or may not be present. There may be nothing in the external appearance or size of the atrium to suggest the abnormality, both atrial appendages being well developed; but usually there is a single atrio-ventricular orifice, confined to the left part of the common atrium, and sometimes the ventricular and bulbar septa are also absent. The condition is not incompatible with life, but is fatal in early childhood. (Full descriptions of specimens are given by SYMINGTON, *Jour. Anat.*, vol. xxxiv.; RUDOLF, *ibid.*; PATERSON, *ibid.*, vol. xli.)

(*b*) *The Atrial Canal.* The right and left atrio-ventricular orifices are separated from one another by a fusion of the anterior and posterior endocardial cushions of this region (p. 58); but this fusion may fail to occur and a common atrio-ventricular orifice persists. This abnormality is rare and is usually associated with other grave cardiac defects and always with the presence of a foramen primum in the atrial septum, the lower margin of which forms a free crescent arching over the atrio-ventricular opening. The atrio-ventricular valve in these cases usually consists of three cusps, the anterior mitral cusp being fused with the anterior tricuspid cusp and the posterior mitral cusp with the septal tricuspid cusp.

(*c*) *The Ventricular Septum.*—The formation of the ventricular septum and the closure of the interventricular foramen by the pars membranacea septi are described on p. 60. The ventricular part of the membraneous septum may fail to form, so that an interventricular foramen persists. The size of the persistent foramen varies from a pin-hole to an inch in diameter. It is bounded below by the muscular ventricular septum, above by the aortic orifice, anteriorly by the interbulbar septum, and posteriorly by a band of fibrous tissue derived from the endocardial cushions of the atrial canal and lying below the non-coronary cusp of the aortic valve; and through it the "inflowing" part of the right ventricle discharges part of its contents.

The muscular part of the septum (septum inferius of His) is probably never entirely absent, though it may be so very imperfectly developed or occupy so abnormal a position that the heart may be well described to be monoventricular. If the septum is poorly developed it forms a muscular ridge between the lower parts of the right and left ventricles; as a rule it is much nearer the right wall. Its upper concave edge is free and bounds a large interventricular foramen. The bulbar and atrial septa may also be absent, there being then a single arterial orifice, usually the aorta, arising from the right (bulbar) part of the ventricle, and a common atrio-ventricular opening into the left part of the ventricle; such a heart was named in an older terminology a bilocular heart. If the pulmonary orifice is also present it is usually stenosed; and in some cases there is a transposition of the arterial stems.

A much more rare abnormality is that in which the septum inferius is so close to one wall of the heart that the ventricle appears to consist of a single

cavity. In these cases the suppressed cavity, which may be either the right or the left ventricle, exists as a cleft in the wall of the larger cavity and communicates with it over the upper edge of the septum; if it is the right ventricle which is suppressed the defect may be only of the body of the ventricle, the infundibular part being well developed. The atrio-ventricular orifice of the suppressed cavity is obliterated, or at the least greatly stenosed. The foramen ovale persists in the atrial septum. A single or double arterial orifice is present, but if two vessels exist one is usually constricted; and the ductus arteriosus remains patent. Instances of this condition are described by LAWRENCE, *Jour. Anat.*, vol. xxxv.; and YOUNG, *ibid.*, vol. xli.

Foramina in the muscular part of the ventricular septum have been described, but are uncommon.

(*d*) *The Bulbar Septum.*—A foramen may be present in the bulbar septum and form a communication between the infundibulum of the right ventricle and the aortic canal of the left ventricle; it lies above the position of the inter-ventricular foramen. The septum which divides the bulbus and the truncus arteriosus may not be developed, so that there is a single arterial orifice and a single arterial stem. In these cases the pulmonary arteries spring from the aorta. It appears well established that the single arterial orifice is guarded by three semilunar cusps, though from the developmental history of the parts four cusps would be expected; (see p. 61; a case is described by KEITH, *Jour. Anat.*, vol. xxxiii.).

THE PERICARDIUM

The pericardium is the fibro-serous sac in which the heart is contained. It is conical in shape, its base resting on the diaphragm and its upper narrow part surrounding the trunks of the great vessels for some distance from the heart. Its wall consists of three layers: (1) The **fibrous pericardium**, a strong and resistant fibrous sac which protects the heart from the surrounding structures. This layer fuses with the diaphragm below and with the outer coats of the great vessels above. (2) The **serous pericardium**, a typical serous membrane which lines the inner surface of the fibrous pericardium and is fixed to it by subserous tissue; from the fibrous pericardium the serous layer is inflected along the great blood vessels to the heart, which, as already described, it invests as the epicardium. The cavity of the serous sac is the **pericardial cavity**. (3) The fibrous pericardium is fixed to the surrounding structures by a layer of **epipericardial fibrous tissue**. This tissue varies in texture, being small in amount and areolar at some places and thick and ligamentous at others, and forming there strong ligaments which fix the pericardium to the surrounding parts; these ligaments specially attach the pericardium to the diaphragm, the sternum, and the vertebral column.

It is most convenient first to describe the fibrous pericardium and its attachments to the surrounding parts.

The **fibrous pericardium** is a dense unyielding membrane composed of bundles of fibrous tissue which interlace in every direction; in its deeper layers there is a network of elastic fibres. The interlacement is best seen on the posterior wall, where the bundles are almost tendinous in appearance; the fibres of the anterior wall are more parallel, and the surface has a white glistening fibrous appearance. The thickness of the membrane varies, the thinnest places being where the great vessels break through it; at these places it is continued round

the vessels in the form of tubular prolongations which gradually become lost on their external coats, so that it is scarcely possible exactly to decide the place of transition. The pulmonary artery and the aorta, the superior vena cava, and the four pulmonary veins receive investments of this kind. The fibrous pericardium is attached below to the upper surface of the diaphragm, partly to the central tendon and partly to the muscle surface of the left side (fig. 75). The connection is very firm in front near the middle line, the tissues of the pericardium and diaphragm being continuous; elsewhere the attachment is more lax and is effected mainly by areolar tissue.

The **fibrous pericardium** is a structure *sui generis*, that is, it is an independent fibrous-tissue stratum and not merely a condensation of the endothoracic fascia as has sometimes been maintained; it receives many accessions from the fibrous tissues surrounding it, but these may be removed and, as at the parts which receive no accessions, it may be displayed as a definite stratum.

The **lateral surfaces** and part of the anterior surface of the pericardium are covered by the mediastinal pleuræ. The union between the two layers is close, there being only a little fibrous tissue interposed; but along the phrenic vessels and nerve, which intervene, the fibrous tissue is looser and may even contain a little fat.

The pleural-free triangular part of the **anterior surface** of the pericardium which lies behind the lower part of sternum and the adjacent left costal cartilages (p. 116) is covered by loose cellular tissue which extends to the overlying chest wall. This precardial tissue contains fat in variable amount, but usually in some quantity in the lower parts where the diaphragm is attached to the sternum; and in it there is a median sagittally placed band, the **inferior sterno-pericardial ligament**, which, however, is sometimes weakly developed. It is attached in front in the region of the sterno-xiphoid junction and extends upwards and backwards and gradually loses itself on the pericardium. At a higher level, in the region of the third intercostal space and between the two pleuræ which here are close together, the fibrous tissue forms a septum in which thickenings (middle sterno-pericardial ligament, LUSCHKA) have been described. Above this position the anterior surface of the pericardium, covering the front of the arterial trunks, is again free, and there is attached to it in the middle line the **superior sterno-pericardial ligament**. This ligament is attached in front to the posterior surface of the manubrium sterni at the insertion of the sterno-thyreoid muscles and on the lateral sides of this to the first costal cartilages; further, some of its fibres (the chief part of the ligament, DEBIERRE and TRAMBLIN) are derived from the middle (pre-tracheal) layer of the cervical fascia, and especially from that part which surrounds the thymus gland.

The **base** of the pericardium rests on the upper surface of the diaphragm and is adherent to it over a triangular area about 10 cm. broad at its base in front and 5 to 6 cm. from front to back. Along the front of this area and at the anterior part of the right side the diaphragmatic fascia is continued into the pericardium so that the pericardium and the diaphragm are intimately united; this connection forms the **phrenico-pericardial ligament**. Over the remaining part of the area of adherence, which corresponds to the central part of the tendon of the diaphragm, except on the left, where it extends for a short distance on to the muscle (fig. 75), the union between the two structures is much less close, the diaphragmatic fascia being continued upwards into the cellular tissue round the aorta and the œsophagus.

In most mammals, the exceptions being the anthropoids, some aquatic forms, and a few isolated species (p. 11), there is no union between the pericardium and the diaphragm, for the right pleural sac extends between them as the **infra-pericardial sinus**; this recess is occupied by the infra-cardial lobe of the right lung. The entrance to the sinus is bounded ventrally by the inferior vena cava and dorsally by the œsophagus (fig. 75). In the gibbon the anterior part of the sinus is obliterated, but the dorsal part persists and contains a small lung rudiment; in the chimpanzee and the orang there is a small slit-like dorsal part of the sinus which is unoccupied, while in the gorilla, as in man, the obliteration is complete. The infra-pericardial sinus is a secondary formation, for in the early stages of development the dorsal wall of the pericardium is fused with the anlage of the diaphragm. In man the sinus is obliterated on account of the shortening of the thorax (TANJA, RUGE), but not infrequently a small lung lobule is to be seen extending behind the inferior vena cava into a short recess between the diaphragm and the pericardium, and though the lobule be absent the recess may be present and contain fat and lymph glands. There must be distinguished from this recess the **infra-cardiac bursa**, which is the persistent cranial end of a diverticulum of the bursa omentalis (BROMAN) and which lies on the right side and on the anterior wall of the œsophagus.

in the development of the diaphragm it is separated from the bursa omentalis and usually disappears at the end of fœtal life (RAVN, HOCHSETTER; and for a fuller description see Z[illegible], *Anat. Anz.*, Bd. liii.).

The base of the pericardium, as is shown in fig. 75, reaches backwards to the anterior circumference of the orifice in the diaphragm for the inferior vena cava. From here the pericardium is, as it were, wrapped round the cava from in front, its lower edges sloping upwards and backwards on each side of the vessel, so that on its posterior wall there is a Λ-shaped area which lies outside the pericardium (fig. 77). The fibrous pericardium is attached to the cava along this line, the posterior attachment being the least strong, especially in children where the right and left halves of the pericardium can be separated; and its fibres gradually fuse with the adventitia of the vein. Hernial protrusions of the serosa are often to be found in this region. On the right side of the inferior vena cava there are to be seen fibrous bands of tendinous nature; these constitute the **right phrenico-pericardial ligament** (of TEUTLEBEN). This ligament is attached below to the diaphragm on the right margin of the caval orifice and passes vertically upwards, more or less covering the right side of the cava, and is inserted into the pericardium on which its fibres may be traced as far as the root of the lung; here it is usually described to divide into two parts, one of which is continued in front and the other behind the root of the lung. Smaller and less constant bands pass to the pericardium from the left and posterior margins of the caval foramen; the posterior bands sometimes contain muscle fibres. The **left phrenico-pericardial ligament** (of TEUTLEBEN) is the name given to a rather weakly developed tract of fibres which is attached to the left margin of the central tendon of the diaphragm and ascends on the left surface of the pericardium as far as the root of the left lung. It is much less easily defined than the right ligament.

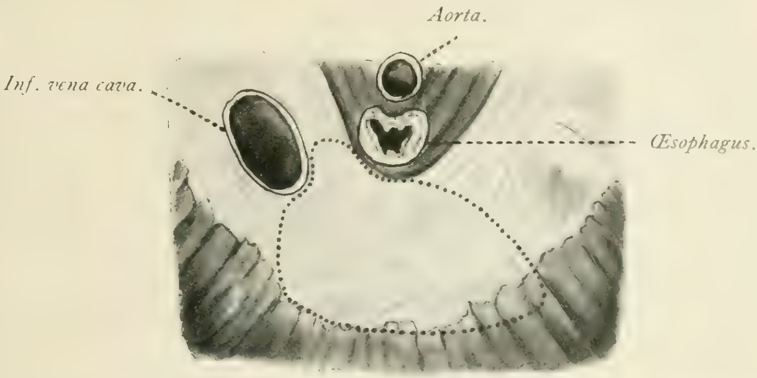


FIG. 75.—THE UPPER SURFACE OF THE DIAPHRAGM WITH THE AREA OF ADHERENCE OF THE PERICARDIUM MARKED ON IT. (After TESTUT.)

The **posterior surface** of the pericardium is in contact with the organs of the posterior mediastinum and is bound to them by very loose connective tissue. In this tissue various thickenings have been described as special ligaments; among others, bands are said to pass from the œsophagus and from the margin of the œsophageal opening in the diaphragm to the pericardium (lig. œsophago-pericardiaca), from the trachea at its bifurcation, and from the left bronchus.

The **apical part** of the fibrous pericardium is continued upwards round the great vessels, the arteries and the veins, and ultimately fuses with their fibrous coats; the line of fusion is irregular, that is, the several vessels are enclosed for different lengths within the fibrous sac. The superior vena cava is enclosed for a distance of about 3·5 cm.; the aorta is enclosed for a distance of 6 to 7 cm., the line of fusion being at the level of, or a little below, the origin of the innominate artery; the pulmonary artery is covered in front up to about the level of its bifurcation, that is, for a distance of about 5 cm., while behind the pericardium reaches the lower border of its right branch and there divides into two layers, one of which passes below the branch and fuses with its wall and the other passes over its posterior surface to reach the aorta (fig. 76); and the extensions on the pulmonary veins from the side parts of the pericardium are short but very variable. Passing to the apical part of the pericardium there are the **vertebro-pericardial ligaments**. These bands apparently are extremely variable in their form, attachments, and size; but, according to TEUTLEBEN, who gave the fullest description of them, they arise from

the prevertebral fascia over the lower cervical and upper thoracic region and pass downwards, one on each side, to the arch of the aorta where they divide into two sets of fibres; the superficial fibres cross the aorta and terminate in the anterior part of the apical region of the pericardium, while the deep fibres descend to the root of the lung and terminate partly in it and partly on the pericardium, becoming continuous there with the phrenico-pericardial ligaments. Many investigators, it should be said, have been unable to identify ligaments conforming to this description.

The **serous pericardium**, or the pericardium proper, has the general characters of a serous membrane. It may be described, therefore, as a closed sac, which is invaginated by the heart, so that two parts, continuous along the line of invagination, may be distinguished; these parts are (1) the **parietal layer** which lines the inner surface of the fibrous pericardium and is closely adherent to it; and (2) the **visceral layer** (the epicardium) which invests the surface of the heart and ensheaths, or partly ensheaths, the great vessels (fig. 76). Both layers are firmly fixed to the overlying tissues, and only at those places where the parietal layer is inflected along the vessels to the visceral layer is

FIG. 76.—DIAGRAM OF A SAGITTAL SECTION OF THE HEART AND PERICARDIUM TO SHOW THE DISPOSITION OF THE SEROUS LAYER.

there a certain looseness of the fixation. This looseness is specially noticeable at the inflection along the aorta and pulmonary artery; along the venæ cavæ the union is more close. The aorta and the pulmonary artery are enclosed together in a complete sheath, but the veins, which are enclosed in a separate sheath, are only partially covered; thus, the superior cava is covered in front and on each side, the pulmonary veins in front and above and below, and the inferior vena cava in front and at the sides. The two sheaths, arterial and venous, are quite separate, that is, there are two inflections of the parietal into the serous layer. It is possible, therefore, when the pericardial sac is opened from the front, to pass the fingers from right to left behind the aorta and pulmonary artery and in front of the atria through a passage which is called the **transverse sinus** of the pericardium (fig. 77).

The Reflections of the Serous Pericardium.—The irregular and complicated lines of the reflections of the parietal into the visceral layer of the pericardium are seen after the vessels are cut across and the heart is removed (fig. 78). A common sheath, it is shown, is carried downwards round the aorta and pulmonary artery, while a second common sheath, much more complicated in its folding, is seen to embrace the four pulmonary veins and the superior and inferior venæ cavæ. Between these two sheaths, the arterial and the venous, there is the narrow strip of the pericardial wall which forms the posterior wall of the transverse sinus.

The arterial sheath surrounds the aorta and is then reflected backwards as a narrow loop to the pulmonary artery, which it also encloses. Two deep pockets of serosa are thus formed, one on the right of the aorta, the **recessus aorticus**, and the other on the left, between the aorta and the pulmonary artery and limited on the left by the ductus arteriosus, the **recessus pulmonalis**. The venous sheath ascends from the inferior caval orifice, leaving a triangular part of the posterior surface of the cava free (fig. 76), to the right pulmonary veins which are surrounded by short deviations of the membrane to the right; the line of reflection then passes almost transversely to the left across the posterior wall of the pericardium to the upper left pulmonary vein, there being from this part an upward extension to the superior cava and a downward extension to

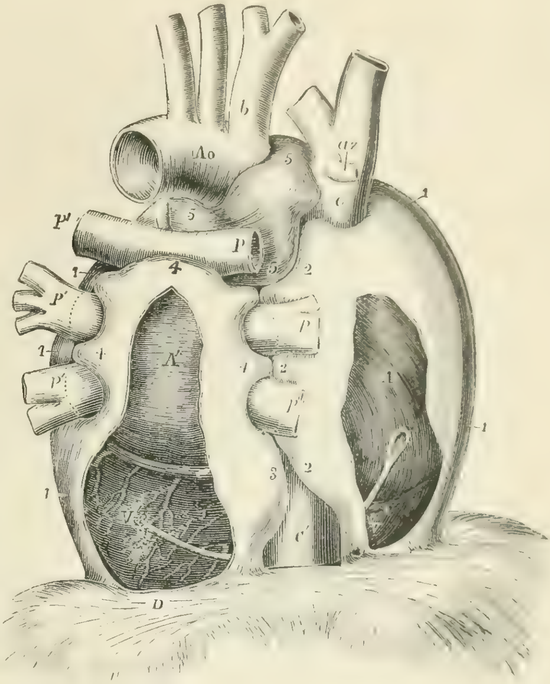


FIG. 77.—SEMIDIAGRAMMATIC VIEW OF THE PERICARDIUM FROM BEHIND, DESIGNED TO SHOW THE PRINCIPAL INFLECTIONS OF THE SEROUS SAC ROUND THE GREAT VESSELS. (ALLEN THOMSON.) $\frac{1}{2}$.

The drawing is taken from preparations in which the heart and vessels had been partially filled by injection, the pericardium inflated and dried in the distended state, and the fibrous continuation on the vessels removed. By the removal of a portion of the pericardium from behind the right and left cavities of the heart, the position of that organ is made apparent. *A*, right atrium; *A′*, left atrium; *V*, right ventricle; *V′*, left ventricle; *Ao*, aortic arch; *b*, innominate artery; *C*, vena cava superior; *az*, azygos vein; *C′*, vena cava inferior; *c″*, great coronary vein; +, ligamentum arteriosum; *P*, right, *P′*, left pulmonary artery; *p*, right, *p′*, left pulmonary veins; *D*, central tendon of diaphragm; 1, sac of pericardium; 2, the portion on the right side which partially surrounds the superior vena cava, the right pulmonary veins, and the inferior vena cava; 3, portion on the left side which partially surrounds the inferior vena cava; 4, portion which is extended upwards behind the left atrium, and partially folds over the pulmonary arteries and veins, meeting between these different vessels the extensions of the sac from the right and left; 5, upper part of the transverse sinus passing behind the aortic and pulmonary arterial trunks. A bent probe is passed within the pericardium from behind the right atrium, in front of the inferior vena cava, to the back of the left ventricle, which may indicate the place where the large undivided sac of the pericardium is folded round that vein.

the lower left pulmonary vein (fig. 78). On the heart wall the attachment of the venous mesentery is along a narrow strip vertically on the right atrium between the venæ cavæ and transversely over the posterior wall of the left atrium.[1] There are deep recesses of the serosa between the two left pulmonary veins and between the superior vena cava and the upper right pulmonary vein and shallower recesses between the two right pulmonary veins and between the lower right pulmonary vein and the inferior vena cava. The **oblique sinus** of the pericardium is the name given to the large diverticulum, which is included within the line of reflection of the venous mesentery; it is entered from below, when the pericardium is opened from the front, by passing

[1] For a discussion of the influence of the fixation of the atria to the pericardium on the action of the heart, see KEITH, *Jour. Anat.*, vol. xxxviii.

the auricles under the heart (figs. 76 to 79). Its upper boundary, the transverse reflection, lies at the level of the right pulmonary artery, but it may extend so far cranialwards as to pass dorsal to the transverse sinus of the pericardium (fig. 76).

The **vestigial fold of the pericardium** (the fold of MARSHALL) is a narrow, sharp semilunar fold of pericardium, the length and height of which are variable; it stretches from the left pulmonary artery, close to its commencement, to the anterior wall of the left atrium; the concave border of the fold is directed forwards. It was first recognised by THEILE, but MARSHALL gave a more accurate description of it and pointed out that it contains the rudiments of the lower end of the left superior vena cava (p. 107). If the fold is well developed its cranial end may be traced over the pulmonary artery to the posterior wall of the pericardium and its lower end over the anterior and upper walls of the left atrium and then on the dorsal wall below and medial to the entrance of the left pulmonary veins until there can be recognised in it the oblique vein of Marshall (p. 107).

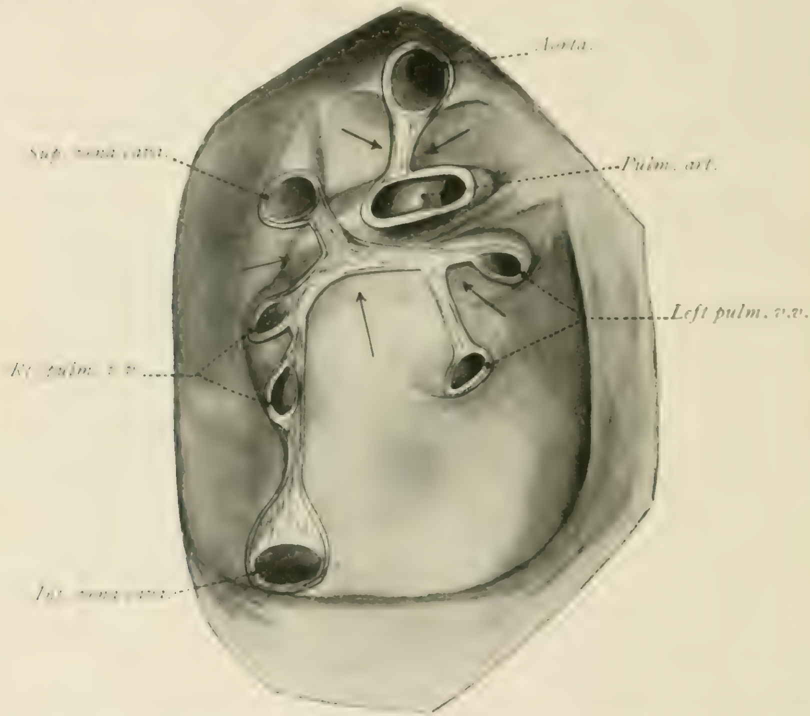


FIG. 78.—THE POSTERIOR WALL OF THE PERICARDIUM, SHOWING THE LINES OF REFLECTION OF THE SEROUS PERICARDIUM. (After TANDLER.)

The **pericardial cavity** is the space between the two layers of the pericardium. The space normally is virtual, that is, the layers are in contact and moistened with a small amount of viscid fluid; but after death some free fluid is usually to be found in it. The capacity of the pericardial cavity, as measured by the amount of fluid which can be injected into it, is about 400 to 600 c.c.; but greater amounts of fluid than this may collect in conditions of chronic pericarditis.

The **arteries** of the fibrous pericardium, which are of small calibre, are derived from the neighbouring vessels, namely, the internal mammary artery and its pericardiaco-phrenic branch, and the superior phrenic and mediastinal arteries. The primary vessels form a plexus in the superficial layers of the pericardium, and from it finer branches ramify through the substance of the membrane and reach the subendothelial layers of the serous membrane (p. 25). The primary plexus anastomoses with the coronary circulation along the aorta and pulmonary artery. The **veins** closely accompany the arteries; the main trunks enter the internal mammary veins in front and the azygos systems behind. The **nerves**, which are slender twigs, are derived from the phrenic, vagus, and sympathetic nerves; a recent account of them is given by FRANCILLON, *Anat. Anz.*, Bd. lxi. The phrenic branches are distributed chiefly on the anterior

surface and the sides; branches from the right vagus descend along the superior vena cava, and from the œsophageal cords of both vagi branches are given to the posterior surface; while the sympathetic fibres arise from the upper thoracic ganglia, the plexuses on the subclavian and phrenic arteries, and the diaphragmatic plexus.

The Development of the Pericardium. The early heart tube, as already described (p. 14), lies in a relatively large cavity, the **pleuro-pericardial cavity**, which is continuous with the headward extensions of the general body cavity, one on each side (see Vol. I.). The inner wall of the pleuro-pericardial cavity forms the myo-epicardial mantle (p. 14); and this is continued backwards, dorsal to the heart, as the dorsal mesocardium, which partially subdivides the cavity into symmetrical halves (fig. 79). The pleuro-pericardial cavity is closed at its headward end, at the sides, dorsally, and ventrally, but caudally there are two openings, one on each side, the **pleuro-peritoneal passages**, which lead into the peritoneal cavity. These passages are bounded on their ventro-medial aspect by the omphalo-mesenteric (vitelline) veins which, covered by the splanchnopleure, pass cranially and dorsally towards the sinus venosus. The splanchnopleure covering these veins has a lateral connection on each side with the somatopleure, and in these connections, which form the dorsal parts of the septum transversum, the ducts of Cuvier pass transversely from the body wall medialwards to the sinus venosus. The septum transversum is a mass of mesoderm which passes dorsally from the anterior edge of the opening of the mid-gut into the yolk-sac, and forms the caudal boundary of the pericardial cavity. The caudal and ventral part of the septum becomes occupied by the developing liver; the cranial and dorsal portion is connected with the heart, the sinus venosus lying in its

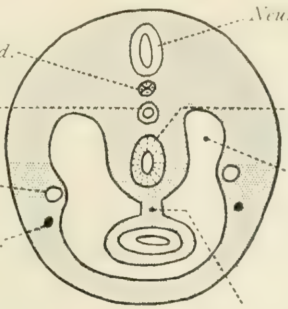


FIG. 79.—A DIAGRAM OF THE PLEURO-PERITONEAL PASSAGES.

dorsal border. Its mesodermic tissue is continuous through the hinder part of the dorsal mesocardium with the mesoderm surrounding the gut-tube, and when the lung bud reaches this level its mesodermic covering fuses with this dorsal extension. There is thus formed what may be termed the mediastinal septum which contains the gut-tube and the primordia of the lungs. Behind the dorsal edge of the septum transversum, and separated from one another by the mediastinal septum, are the pleuro-peritoneal passages. These passages are very much narrowed from in front by the ducts of Cuvier as they pass medially to the sinus venosus and now open from the dorsal parts of the caudal wall of the pleuro-pericardial cavity (fig. 79). As already described, the posterior mesocardium disappears, so that the heart tube now stretches across a single cavity, from behind where the sinus venosus embedded in the septum transversum enters the cavity, to in front where the bulbus cordis pierces its cranial wall (fig. 80). The thin ventral wall of the pericardium, formed of mesoderm covered with ectoderm, reaches caudally to the septum transversum.

It has already been explained that in the further development of the heart, and associated with its caudal displacement, the sinus venosus separates itself from the septum transversum and, with its horns, shifts from the caudal end of the heart tube to the dorsal surface of the atrium; and that with this change the two horns of the sinus which originally formed with the transverse part an arc convex cranially now run from before backwards and form an arc convex caudally (p. 17 and fig. 12). This change in the position of the sinus horns, and of the ducts of Cuvier opening into them, alters the position of the dorsal edge of the septum transversum, carrying it in a cranial direction so that the septum now forms a considerable part of the dorsal wall of the pericardium, as well as its caudal wall, and the pleuro-peritoneal passages open from the front part of the cavity; and, further, the dorsal edge of the septum forms the ventral and lateral boundaries of the passages (fig. 81). The ducts of Cuvier, at this time, are becoming more and more raised, in a medial direction, from the body wall, and as development proceeds

apparently approach nearer and nearer to one another on the dorsal aspect of the heart: the active growth process, as Brachet has pointed out, is an increase in the transverse diameter of the pericardial cavity, and the result is that the ducts, which remain in their original position, now lie in the free edges of two folds, the pleuro-pericardial folds. The original simple pleuro-pericardial cavity is thus divided into an anterior pericardial part and two dorsal pleural parts, the latter of which are partially separated from one another by the fore-gut and the lung rudiment. In the following stages of development the free edges of the pleuro-pericardial folds containing the ducts of Cuvier fuse with the dorsal surface of the atrium, so that the pericardial cavity is closed dorsally (fig. 82); the fusion occurs to a much greater extent on the left than on the right side, for on the right side there occurs the absorption of the sinus into the right atrium, as already described. This fusion having taken place the original rather wide passage across the pericardium between the bulbus cordis in front and the sinus behind is very much narrowed; it is now the definitive transverse sinus of the pericardium.

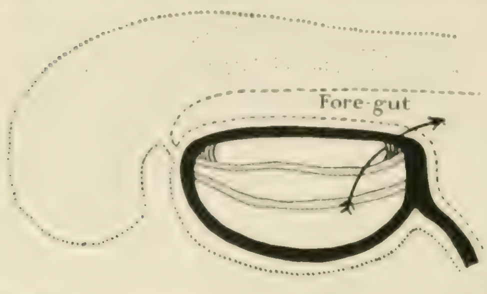


FIG. 80.—A DIAGRAM OF A LONGITUDINAL SECTION OF THE EARLY HEART AND PERICARDIUM. The arrow is in one of the pleuro-peritoneal passages.

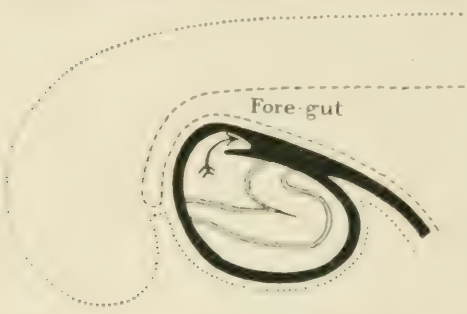


FIG. 81.—A DIAGRAM OF A LONGITUDINAL SECTION OF THE EARLY HEART AND PERICARDIUM AT A LATER STAGE THAN FIG. 80. The arrow is directed into the pleuro-peritoneal passage.

The free edge of the pleuro-pericardial fold now also fuses with the mesoblastic covering of the root of the expanding lung rudiment, the fusion first occurring at the caudal end where the septum transversum is already fused with it; the pericardial and the pleural cavities are thus completely separated. The pleural cavities at this stage lie entirely on the dorsal side of the pericardial cavity (fig. 82), but with the growth of the lungs they gradually extend forwards, on the lateral sides of the phrenic nerves, burrowing into the anterior body wall, and splitting it into two layers, of which the deeper becomes the fibrous pericardium and its serous lining (fig. 83).

The lines of reflection of the parietal into the visceral layer of the serous pericardium are most easily understood by a reference to the changes which occur during the development of

FIG. 82.—A DIAGRAM TO SHOW THE FORMATION OF THE PLEURO-PERICARDIAL FOLDS.

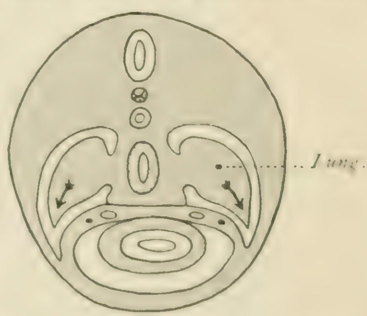


FIG. 83.—A DIAGRAM TO SHOW THE DEVELOPMENT OF THE PLEURAL CAVITIES.

the heart. In the earliest stages (fig. 84, A) the parietal layer of the pleuro-pericardial cavity is continued into the myo-epicardium (*a*) round the sinus venosus (S.V.) and (*b*) round the bulbus cordis (B.), and these structures are separated by a wide interval, the transverse sinus of the pericardium. In the succeeding stage (fig. B.) the pulmonary vein (P.V.) enters the left

atrium through the dorsal mesocardium, and the opening of the sinus is shifted to the right. Later, as was previously described, the stem of the pulmonary vein is absorbed into the left atrium and the sinus venosus into the right atrium, so that there are distinct openings of right and left pulmonary veins and of superior and inferior venæ cavae; and the line of the pericardial reflection is carried round these openings and the posterior mesocardium is greatly broadened (fig. C). At the same time the bulbus divides into the pulmonary artery and the aorta. The transverse sinus of the pericardium is greatly narrowed. The adult condition (fig. D) is reached by the further absorption of the stems of the pulmonary veins into the left atrium until there are two openings on each side, those of the right side being projected to the right beyond the line between the superior and inferior cavæ; and between the openings of each side there is a narrow strip of reflection which forms the upper boundary of the oblique sinus of the pericardium.

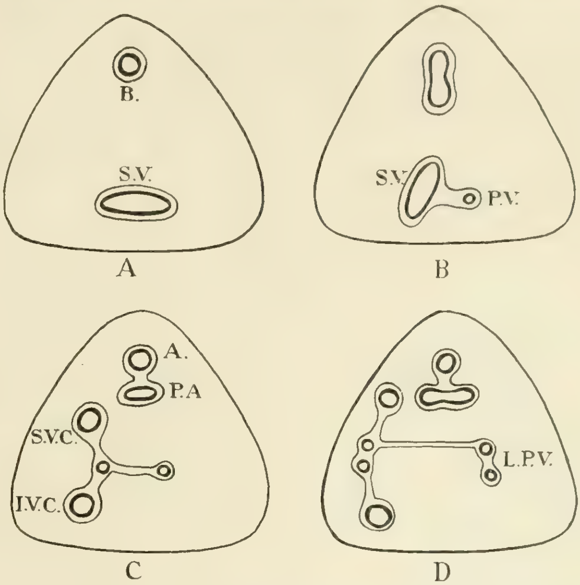


FIG. 84.—DIAGRAMS OF THE DORSAL WALL OF THE PERICARDIUM TO SHOW THE CHANGES DURING THE DEVELOPMENT OF THE HEART IN THE LINES OF REFLECTION OF THE SEROUS PERICARDIUM.

The reflection is then carried upwards on the pulmonary artery to its bifurcation and on the aorta to the level of the origin of the innominate trunk.

Defects of the Pericardium.—A considerable number of cases of congenital deficiency of the left side of the pericardium have now been recorded; PERNA (*Anat. Anz.*, Bd. xxxv.) and PLAUT (*Frankfurt Zeitschr. f. Path.*, Bd. xii.) have collected and summarised the literature, and recent cases are described by KEITH (*Jour. Anat.*, vol. xli.), CHASE (*ibid.*, vol. l.), and M'GARRY (*Anat. Record*, vol. viii.). The defects are in the lateral wall of the fibrous pericardium and its serous lining behind the phrenic nerve and in front of the root of the lung; all the recorded cases have been on the left side. The openings in the pericardium have been of various sizes, sometimes as small as ¼ in. in diameter, but sometimes so large that the whole lateral wall is defective and the left lung and the heart lie in a common serous cavity; the visceral pericardium is then in contact with the visceral pleura and frequently there are adhesions between them. The condition represents a persistence and enlargement of the pleuro-pericardial foramen, possibly due to an early atrophy of the left duct of Cuvier (PERNA). It is commonly associated with other developmental defects.

LITERATURE ON THE HEART

Aagaard, O. C. . . Les vaisseaux lymphatiques du Cœur. Copenhagen, 1924.

Aagaard, O. C., and Hall, H. C. Über Injectionen des Reisleitungssystem. *Anat. Hefte*, Bd. 51, 1914.

Ackerknecht, E. . . Die sogenannte abnormen Sehnenfäden des menschlichen Herzens. *Anat. Anz.*, Bd. 56, 1923.

Albini, F. . . . . Ueber die Noduli an den Atrioventrikularklappen des Menschen. *Wochenschr. d. k. k. Ges. d. Aertze in Wien.*, 2 Jahrg., 1856, No. 26.

Albrecht, E. . . . Der Herzmuskel und seine Bedeutung für Physiologie, Pathologie, und Klinik des Herzens. Berlin, 1903.

Alfandary, I. . . . Sur la persistance du sinus veineux chez le fétus humain. *Arch. de Anat.* (Strassburg), Tome vii., p. 65, 1927.

Amenomiya, R. . . Beziehungen zwischen Coronararterien und Papillarkuskel im Herzen. *Virchow's Arch.*, Bd. 199, 1910.

Argaud, Fr. . . . Sur le tendon de Todaro et la structure de la valvula Eustach chez l'homme. *C. R. Soc. Biol.* Paris, 1911.

,, ... Sur l'innervation de la zone auriculaire droite qui répond à l'origine de la systole cardiaque. *Ibid.*, 1911.

,, ... Sur l'appareil nerveux et la structure de la valvule d. Thebes. chez l'homme. *Ibid.*, 1911.

,, ... Sur la vascularisation des valvules auriculo-ventriculaires chez le cheval. *Ibid.*, T. 72, 1912.

,, ... Sur le tænia terminalis du cœur humain. *Ibid.*, T. 72, 1912.

,, ... Sur la structure de la bandelette ansiforme. *Ibid.*, 1912.

Arnold, J. . . . . Zur Morphologie des Glykogens im Herzmuskel. *Arch. f. mikrosk. Anat.*, Bd. 73, 1909.

,, ... Purkinjesche Fasern. *Sitzungsbericht d. Heidelberger Akad. d. Wissensch.*, 1909.

Aschoff, L. . . . . Die Nervengeflechte des Reizleitungssystems. *Deutsche med. Wochenschr.*, 1909; *Naturf. Ges. Freiburg*, 1909.

,, ... Über den Glykogengehalt des Reizleitungssystems. *Verk. d. D. Path. Ges. Tag.*, 12, 1908.

,, ... Ueber die neueren anatomischen Befunde am Herzen und ihre Beziehungen zur Herzpathologie. *Med. Klinik*, 1909.

Athanasiu et Dragoiu . Association des éléments élastiques et contractiles dans le myocarde des Mammiféres. *C. R. Soc. Biol.*, T. 70.

Azoulay, L. . . . Les nerfs du cœur chez l'homme. *C. R. Soc. Biol.*, Sér. 10.

Babes, J. . . . . Observations sur le fibres musculaires du cœur. *C. R. Soc. Biol.*, T. 64.

Banchi, A. . . . . Morphologia delle arteriæ coronariæ cordis. *Arch. Ital. di Anat. e Embriol.*, vol. iii., 1904.

Bayne-Jones, A. . . Blood Vessels of the Heart Valves. *Amer. Jour. Anat.*, vol. xxi., 1917.

Beddard, F. E. . . Mammalia. 1902.

Beitzke, H. . . . Ueber die sogenannten weissen Flecken am grossen Mitralsegel. *Virchow's Arch.*, Bd. 163, 1903.

Benninghoff, A. . . Ueber die Beziehungen des Reisleitungssystem und der Papillarmuskeln zu den Konturfasern des Herzschlauchs. *Anat. Anz.*, Bd. 37, 1923.

Berkley, J. . . . The Intrinsic Nerve Supply of the Cardiac Ventricles in certain Vertebrates. *The Johns Hopkins Hospital Reports*, vol. vi., 1894.

Berkley, J. — On Complex Nerve Terminations and Ganglion Cells in the Muscular Tissue of the Heart Ventricle. *Anat. Anz.*, 1894.

Bernays, A. C. — Entwicklungsgeschichte der Atrioventricularklappen. *Morphol. Jahrb.*, Bd. 2, 1876.

Berti, M. — Die Theorie von Haushalter und Thiry uber die Blutknotchen der Herzklappen Neugeborner. *Arch. f. Kinderheilk.*, Bd. 31, 1901.

Bischoff, A. — Einige Gewichts und Trockenbestimmungen der Organe des menchlichen Korpers. *Zeitschr. f. rat. Med.*, 3 R., Bd. 20.

Bock, R. — Die Lymphgefasse des Herzens. (*Vorl. Mitteil.*) *Anat. Anz.*, Bd. 27, 1905.

Boeke, J. — Beiträge zur Kenntnis der motorischen Nervenendigung. *Internat. Monatsschr. f. Anat. u. Phys.*, Bd. 28.

" — The Innervation of the Muscle Fibres of the Myocardium. *Proc. Roy. Acad. Sci. Amsterdam*, vols. xxvii. and xxviii.

Born, G. — Beiträge zur Entwicklungsgeschichte des Säugetierherzens. *Arch. f. mikrosk. Anat.*, Bd. 33.

Brachet, A. — Die Entwicklung der grossen Korperhohlen und ihre Trennung voneinander (Pericardial-, Pleural-, und Peritonealhohle). Die Entwicklung der Pleuropericardial-membran und des Zwerchfelles. *Ergebn. d. Anat. u. Entwicklungsgesch.*, Bd. 7, 1897.

Bräunig, K. — Ueber muskulöse Verbindungen zwischen Vorkammer und Kammer des Herzens. *Berl. klin. Wochenschr.*, Jahrg. 41, No. 38.

" — Ueber muskulose Verbindungen zwischen Verkammer und Kammer bei verschiedenen Wirbeltierherzen. *Arch. f. Anat. u. Physiol.*, Physiol. Abt. 1904, Suppl. Bd., 1 Hälfte.

Bromann, V. — Ueber die normale Existenz einer . . . dritten Pleurahohle (Bursa infracardiaca) beim erwachsenen Menschen. *Anat. Anz.*, Bd. 26.

Brown, M. — Construction of the Ventricles in the Mammalian Heart. *Jour. of Anat.*, vol. xxiii., 1889.

Bundschuh, A. — Blutknötchen an den Herzklappen Erwachsener. *Frankf. Zeitschr. f. Pathol.*, 1910.

Burian, F. — Zur Histologie des Sinusknotens des menschlichen Herzens. *Anat. Anz.*, 59, 1925.

Cady, L. D. — The Sino-ventricular Bundle of the Rabbit's Heart. *Anat. Record*, vol. xxi., 1921.

Campbell, J. — The Coronary Arteries of the Heart. Thesis. Belfast, 1928.

Clark, A. J. — Comparative Physiology of the Heart. Cambridge, 1927.

Coen, E. — Ueber die Blutgefasse der Herzklappen. *Arch. f. mikrosk. Anat.*, Bd. 27.

Cohn, A. — On the Auriculo-nodal Junction. Heart, Vol. I. Observations on Injected Specimens of the Conductive System in Ox Hearts. Heart, Vol. IV.

Cohn und Trendelenburg — Untersuchungen zur Physiologie des Uebergangsbundels am Saugetierherzen nebst mikroskopischen Nachprufungen. *Pflüger's Arch.*, Bd. 131, 1910.

Curran, E. J. — A Constant Bursa in Relation with the Bundle of His; with Studies of the Auricular Connection of the Bundle. *Anat. Anz.*, Bd. 35; *Anat. Record*, vol. iii., 1909.

Darier, J. — Les vaisseux des valvules du cœur chez l'homme à l'état normal et à l'état pathologique. *Arch. de Physiol.*, 1888, No. 5.

Debierre et Tramblin — Etude du péricard. *Jour. de l'Anat. et de la Physiol.*, 1908.

De Gaetani, L. — Ricerche e considerazioni sul fascio atrio-ventricolare. *Atti. Soc. Tosc. Sc. Nat. Pisa, Mem.*, vol. xxvii., 1911.

Il fascio atrio-ventricolare nell'uomo. *Anat. Anz.*, Bd. 39.

Dogiel, J. — Die Ganglienzellen des Herzens bei verschiedenen Tieren und beim Menschen. *Arch. f. mikrosk. Anat.*, Bd. 14, 1877.

" — Die Nervenzellen und Nerven des Herzventrikels beim Frosch. *Ibid.*, Bd. 21, 1882.

Dogiel, J. . . . . Die sensiblen Nervenendigungen im Herzen und in den Blutgefassen der Säugetiere. *Arch. f. mikrosk. Anat. u. Entw.-Gesch.*, Bd. 52.

,, ... Die Bedingungen d. automatischen-rhythmischen Herzkontraktion. *Pflüger's Archiv.*, Bd. cxxxv.

Dogiel, A. S. . . . Zur Frage über den feineren Bau der Herzganglion des Menschen und der Säugetiere. *Arch. f. Anat. u. Entw.-Gesch.*, Bd. 53.

Dogiel und Tumānzew Zur lehre über das Nervensystem des Herzens. *Arch. f. mikrosk. Anat.*, Bd. 36.

Drennan, M. R. . . The Atrio-ventricular Bundle in the Bird's Heart. *Brit. Med. Jour.*, vol. i., p. 321, 1927.

Engel, I. . . . . Beiträge zur normalen und pathologischen Histologie des Atrioventrikularbündels. *Beitr. z. pathol. Anat. u. allg. Pathol. v. Ziegler*, Bd. 48, 1910.

Erlanger, J. . . . Observations on the Physiology of Purkinje Tissue. *Amer. Jour Phys.*, vol. xxx., 1912.

Ewald, E. . . . . Die Funktion der Noduli Arantii. *Berl. klin. Wochenschr.*, 1905.

Fahr, A. . . . . Zur Frage der atrioventrikulären Muskelverbindung im Herzen. *Verhandl. d. Deutsch. Pathol. Ges.*, 12. *Tagung.* Kiel, 1908.

,, ... Ueber die sogenannten Klappenhämatome am Herzen der Neugeborenen. *Virchow's Arch.*, Bd. 184, 1906.

,, ... Das elastische Gewebe im gesunden und im kranken Herzen und seine Bedeutung für die Diastole. *Ibid.*, Bd. 185.

,, ... Ueber die muskuläre Verbindung zwischen Vorhof und Ventrikel im normalen Herzen. *Ibid.*, Bd. 188, 1907-8.

Fedorow, V. . . . Ueber die Entwicklung der Lungenvene. *Anat. Anz.*, Bd. 32.

Firket, P. . . . . De la présence du faisceau interauriculoventriculaire (faisceau de His) chez l'homme. *Compt. rend. Assoc. des Anat.*, 10 Réunion, Marseille, 1908.

Flack, M. . . . . The Sino-auricular Node. *Jour. Physiol.*, vol. xxii., 1910.

Frazer, J. E. . . . The Formation of the Pars Membranacea Septi. *Jour. Anat.*, vol. li., 1916.

Fritsch, R. . . . Herzhypertrophie, Gravid. *Arch. Gynäkol.*, Bd. 10.

Fukutake, K. . . . Beiträge zur Histologie und Entwicklungsgeschichte des Herznervensystems. *Zeitsch. fur gesam. Anat.*, Abt. 1, Bd. 76, 1925.

Gaskell, W. H. . . On the Innervation of the Heart. *Jour. Physiol.*, vols. iv. and v., 1885.

Gaupp, E. . . . . Anatomie des Frosches von Ecker und Wiedersheim, 1896.

Gegenbaur, C. . . . Zur vergleichenden Anatomie des Herzens. *Jenaische Zeitschr. f. Med.*, Bd. 2, 1866.

Gerard, G. . . . . Les cordages tendineux des ventricules du cœur. *Compt. rend. Assoc. des Anat.*, 10 Réunion, Marseille, 1908.

Gibson, A. . . . . On the Primitive Muscle Tissue of the Human Heart. *Brit. Med. Jour.*, 1909.

Greenfield, J. . . . Deficiency of Upper Part of Atrial Septum with Patent Foramen Ovale. *Jour. Anat. and Physiol.*, vol. xxiv.

Greil, A. . . . . Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Herzens und des Truncus arteriosus Wirbeltiere. Leipzig, 1903; and *Morph. Jahrb.*, 31, 1903.

Gross, J. . . . . The Blood Supply to the Heart. New York, 1921.

Gussenbauer, J. . . Ueber die Muskulatur der Atrioventrikularklappen. *Sitzungsber. d. K. Akad. der Wiss. in Wein*, Bd. 57.

Haas, G. . . . . Ueber die Gefässversorgung des Reizleitungssystems des Herzens. *Anat. Hefte*, Bd. 43, Heft 131.

Hannes, F. . . . Untersuchungen über die sogenannten Klappenhämatome. *Arch. f. Pathol. Anat.*, Bd. 193.

Hart, C. . . . . Ueber die Defekte im oberen Teil der Kammerscheidewand des Herzens mit Berücksichtigung der Perforation des häutigen Septums. *Virch. Arch.*, Bd. 181.

Haushalter et Thiry — Études sur les hématomes des valvules auriculoventriculaires dans l'enfance. *Arch. de Méd. expér.*, 1898.

Heidloff, M. — Ein Fall von abnormem Ursprung der Arteria coronaria cordis sinistra aus der Arteria pulmonalis. Diss., Leipzig, 1926.

Herxheimer, G. — Missbildungen des Herzens. Schwalbe, *Die Morphologie d. Missb. d. Menschen u. d. Tiere*, 1910.

L'Heureux, M. — Circulation artérielle auriculaire, ses rapports avec le faisceau de His. Lille, 1912.

Hinze, Fr. — Ueber den Verschluss des Foramen ovale des Herzens. Diss., Berlin, 1893.

Hirsch, C. — Ueber die Beziehungen zwischen dem Herzmuskel und der Korpermuskulatur und über sein Verhalten bei Herz hypertrophie. *Arch. f. klin. Med.*, Bd. 64.

Hirsch, C., und Spalteholz, W. — Coronararterien und Herzmuskelarterien. Anatomische und experimentelle Untersuchungen. *Deutsche med. Wochenschr.*, Jahrg. 33, No. 20.

His, W. — Beiträge zur Anatomie des menschlichen Herzens. Leipzig, 1886.

" — Anatomie Menschlicher Embryonen. Leipzig, 1880-85.

" — Mitteilungen zur Embryologie der Säugetiere und des Menschen. *Arch. f. Anat. u. Physiol.*, 1881.

His, W. (jun.) — Die Tätigkeit des embryonalen Herzens und deren Bedeutung für die Lehre von der Herzbewegung beim Erwachsenen. *Arb. aus. d. med. Klinik zu Leipzig*, 1893.

His (jun.) und Romberg — Beiträge zur Herzinnervation. *Arb. aus. d. med. Klinik zu Leipzig*, 1893.

Hochstetter, F. — Ueber das Vorkommen von Ductus pericardiacoperitoneales bei Kaninchenembryonen. *Anat. Anz.*, Bd. 29, No. 1/2.

" — Die entwicklung des Blutgefässystems. *Hertwig. Handb. d. Entwicklungsgeschichte d. Wirbeltiere*, Bd. 3, Abt. 2.

" — Ueber die Pars membranacea septi. *Vortrag gehalten in d. Wiss. Aerzteges. zu Innsbruck. Wien. klin. Wochenschr.*, 1898.

Hofmann, H. K. — Beitrag zur Kenntnis der Purkinjeschen Fäden im Herzmuskel. Würzburg, 1902.

Holl, M. — Makroskopische Darstellung des atrioventrikularen Verbindungsbündels am menschlichen und tierischen Herzen. Wien, 1911.

Holmes, A. H. — The Auriculo-ventricular Bundle in Mammals. *Jour. Anat.*, vol. lv., 1921.

Horand, R. — Le faisceau arqué du moderator band du ventricule droit du cœur de l'homme et de grand quadrupédes domestiques. *Bull. et Mém. Soc. anat. de Paris*, Année 83.

Humblet, J. — Le faisceau musculaire interauriculo-ventriculaire. *Bull. Acad. de Belgique*, 1904.

Jager, A. — Ueber die Bedeutung des Keith-Flack-Knoten. *Deutsch. Arch. f. klin. Med.*, Bd. 100, 1910.

Jarisch, A. — Pars membranacea septi ventriculorum des Herzens. *Sitzungsber. d. K. Akad. der Wiss. Wien.*, Bd. 120, Heft 5, 1911; *ibid.*, Bd. 121, 1912.

Johnstone, P. N. — Studies of the Atrio-ventricular Bundle with Polarised Light. *Anat. Record*, vol. xxvi., 1923.

" — On the Comparative Vascularity of the Heart Muscle and Purkinje Fibres. *Anat. Record*, vol. xxiv., 1923.

Johnstone, P. N., and Wakefield, F. H. — On the Character of the Purkinje Fibres in Various Regions of the Atrio-ventricular Bundle. *Anat. Record*, vol. xxiv., 1923.

Jones, Tudor — Intra-muscular Nerve Elements of the Ventricular Muscle. *Jour. Anat.*, vol. lxi., 1927.

v. Kahlden — Klappenhämatome des Herzens. *Ziegler's Beitr.*, Bd. 21, 1897.

Karfunkel, R. — Bestimmungen der wahren Lage und Grosse des Herzens und der grossen Gefasse durch Rontgenstrahlen. *Zeitschr. f. klin. Med.*, Bd. 43.

Keith, A. — Abstract of the Hunterian Lectures on the Evolution and Action of Certain Muscular Structures of the Heart. *Lancet*, vol. i., 1904.

Keith, A. . . . The Anatomy of the Valvular Mechanism Round the Venous Orifices of the Right and Left Auricles, with some Observations on the Morphology of the Heart. *Proc. Anat. Soc. of Great Britain and Ireland. Journ. Anat. and Physiol.*, vol. xxxvii., 1902.

,, . . . Malformations of the Heart. *Lancet*, vol. ii., 1909.

,, . . . The Bulbus Cordis of the Human Heart. *Lancet*, vol. ii., 1924.

Keith and Flack . . The Auriculo-ventricular Bundle of the Human Heart. *Lancet*, vol. ii., No. 6, 1906.

,, ,, . . The Form and Nature of the Muscular Connection between the Primary Divisions of the Vertebrate Heart. *Journ. Anat. and Physiol.*, vol. xli., 1905.

Keith and Mackenzie . Recent Researches on the Anatomy of the Heart. *Lancet*, vol. i., 1910.

Kent, A. F. S. . . Researches on the Structure and Function of the Mammalian Heart. *Jour. of Phys.*, vol. xiv., 1893.

,, . . Structure of Cardiac Tissue at the A.V. Junction. *Jour. of Phys.*, vol. xlvii., 1913; also *Quar. Jour. Exp. Phys.*, vol. vii., 1913-14.

Kerr, Graham J. . . A Note on the Morphology of the Heart. *Trans. Roy. Physiol. Soc. Edin.*, 1912.

,, ,, . . Embryology of Vertebrates. 1919.

King, M. R. . . The Sino-ventricular System. *Amer. Jour. of Anat.*, vol. xix., 1916.

Knower, M. . . . Demonstration of the Interventricular Muscle Bands of the Adult Human Heart. *Anat. Record*, vol. ii., 1908.

Koch, W. . . . Zur pathologischen Anatomie der Rhythmusstörungen des Herzens. *Berl. klin. Wochenschr.*, 1910.

,, . . . Ueber das Ultimum moriens des menschlichen Herzens. Ein beitrag zur Frage des Sinusgebietes. *Ziegler's Beitr.*, 1907.

,, . . . Ueber die Struktur des oberen Cavatrichters. *Deutsche med. Wochenschr.*, 1909.

,, . . . Ueber die Blutversorgung des Sinusknotens und etwaige Beziehungen des letzteren zum Atrioventrikularknoten. *Münch. med. Wochenschr.*, 1909.

,, . . . Weitere Mitteilung über den Sinusknoten des Herzens. *Verh. d. Deutsch. Pathol. Ges.*, Leipzig, 1909, 13 Tag.

,, . . . Zur Anatomie und Physiologie der Intracardialen motorischen Zentren des Herzens. *Med. Klinik*, 1912.

,, . . . Der functionelle Bau des menschlichen Herzens. Berlin, 1922.

Krause, W. . . . Die Blutgefässe der Herzklappen. (Historische Bemerkungen.) *Internat. Monatsschr. f. Anat.*, Bd. 6.

Krehl, L. . . . Beiträge zur Kenntnis der Füllung und Entleerung des Herzens. *Abh. d. Kgl. Sächs. Ges. d. Wiss., math.-phys. Klasse*, Bd. 17.

Krehl und Romberg . Ueber die Bedeutung des Herzmuskels und der Herzganglien für die Herztätigkeit des Säugetieres. *Arb. a. d. med. Klinik zu Leipzig*, 1893.

Külbs, F. . . . Das Reisleitungssystem im Herzen. Berlin, 1913.

Külbs und Lange, W. . Anatomische und experimentelle Untersuchungen über das Reizleitungsystem im Eidechsenherzen. *Zeitschr. f. exper. Pathol. u. Ther.*, Bd. 8.

Lange, W. . . . Ueber das Reizleitungsbündel des Herzens. *Sitzungsber., d. Ges. naturf. Freunde*, 1907.

Langendorff, O. . . Zur Kenntnis des Blutlaufes in den Kranzgefässen des Herzens. *Arch. f. d. ges. Phys.*, Bd. 78.

,, . . Ueber die Innervation der Coronargefässe. *Zentralbl. f. Phys.*, 1907.

Langer, A. . . . Ueber die Entwicklungsgeschichte des Bulbus cordis bei Amphibien und Reptilien. *Morph. Jahrb.*, Bd. 21, 1894.

Langer, L. . . . Anastomosen der Coronararterien. *Sitzungsber. d. Kais. Akad. d. Wissench.*, 1880.

,, . . Ueber die Blutgefässe der Herzklappen. *Ibid.*, Bd. 82, 1880; *Virchow's Arch.*, Bd. 109.

Lannelongue, M. Circulation veineuse des parois auriculaire du cœur. Thèse. 1867.

.. Recherches sur la circulation des parois du cœur. *Arch. de Physiol. norm. et path.*, T. 1, 1868.

Laubry et Pezzi Maladies congénitales du cœur. Paris, 1921.

Lauenstein, A. Varietät der Klappen des rechten Atriums. *Virchow's Arch.*, Bd. 68.

Laurens, H. The Atrio-ventricular Connection in Reptiles. *Anat. Record*, vol. vii., 1913; *ibid.*, vol. ix., 1915.

Lewis, T. The Mechanisms of the Heart Beat. London, 1911.

.. The Pacemaker of the Mammalian Heart. *Internat. Cong. of Med.*, London, 1913.

.. The Excitatory Process in the Dog Heart. *Phil. Trans. Roy. Soc.*, London, Ser. B. 206.

Lhamon, R. M. The Sheath of the Sino-ventricular Bundle. *Amer. Jour. Anat.*, vol. xiii., 1912.

Lissauer, M. Fragmentation des Herzens. *Virchow's Arch.*, Bd. 205.

.. Ueber die Lage der Ganglienzellen des menschlichen Herzens. *Arch. f. mikr. Anat.*, 1909.

Loeb u. Magnus, R. Die Form der Kammerhöhlen des systolischen und diastolischen Herzens. *Arch. f. exper. Pathol. u. Pharm.*, Bd. 1.

Longworth, J. Ueber den Grund der Dreizahl der Semilunarklappen. *Klinik*, vol. xiv.

Looser, E. Ueber Netzbildungen im rechten Vorhof des Herzens. Dissert., Zürich, 1902.

Luschka, H. Die Struktur der halbmondförmigen Klappen des Herzens. *Arch. f. phys. Heilkunde*, 1856.

.. Die Blutgefässe der Klappen des menschlichen Herzens. *Sitzungsber. d. Kais. Akad. d. Wissench. Wien, Mathem.-naturew. Kl.*, 1859; und *Virchow's Arch.*, 1852.

.. Die fibrösen Bänder des Herzbeutels. *Zeitschr. f. rat. Med.*, 3 Reihe, Bd. 4.

.. Die Blutergüsse im Gewebe der Kerzklappen. *Virchow's Arch.*, 1857.

MacCallum, J. B. On the Muscular Architecture and Growth of the Ventricles of the Heart. *Johns Hopkins Hosp. Rep.*, vol. ix., 1900.

M'Clure, C. F. Venous System of Didelphys Marsupialis. *Amer. Jour. Anat.*, vol. ii.

Mackenzie, I. Zur Frage eines Koordinationssystem im Herzen. *Verhand. d. Deutsch. Path. Gesellsch.*, 1910.

.. The Excitatory and Connecting Muscular System of the Heart. *Internat. Cong. of Med.*, London, 1913.

Mackenzie, I., and Robertson, J. Recent Researches on the Anatomy of the Bird's Heart. *Brit. Med. Jour.*, vol. ii., 1910.

Mall, F. P. On the Muscular Architecture of the Ventricles of the Human Heart. *Amer. Jour. Anat.*, vol. xi., 1911.

.. Bifid Apex of the Human Heart. *Anat. Record*, vol. vi., 1910.

.. On the Development of the Human Heart. *Amer. Jour. Anat.*, vol. xiii., 1912.

Marcus, H. Über die Innervation des Herzmuskels. *Anat. Anz.*, Bd. 59, 1925.

Marshall, J. B. On the Development of the Great Anterior Veins in Man and Mammalia, etc. *Phil. Trans. Roy. Soc. London*, 1850.

Meigs, A. The Penetration of the Muscular Fibres of the Human Heart by Capillaries, and the Existence in that Organ of very large Capillaries. *Jour. Anat. and Phys.*, vol. xxxiii., 1899.

Meiklejohn, J. The Innervation of the Nodal Tissue of the Mammalian Heart. *Jour. Anat.*, vol. xlviii., 1913.

.. The Topography of the Intracardiac Ganglia of the Rat's Heart. *Jour. Anat.*, vol. xlviii., 1913.

Meinhardt, A. Ueber die Entstehung der Herzklappenhämatome bei Neugeborenen. *Arch. f. Pathol. Anat.*, Bd. 192.

Mergoni, T. Il fascio atrioventricolare di His. *Boll. d. Soc. med. di Parma*, Sér. 2, Anno 3.

Merkel, H. Zur Kenntnis der Kranzarterien des menschlichen Herzens. *Verh. d. Deutsch. Path. Ges.* 10 Tagung, Stuttgart, 1906.

Meyer, A. W. . . Injections of Bundle of His. *Science* (N.S.), vol. xlii., 1915.

Michailow, S. . . Die Nerven des Endocardiums. *Anat. Anz.*, Bd. 32, 1908.

,, . . Zur Frage über den feineren Bau des intracardialen Nervensystem der Säugetiere. *Internat. Monatsschr. f. Anat. u. Phys.*, Bd. 25, 1908.

Mills, A. . . . Action of Reptile Heart and Nerve Supply. *Jour. Anat. and Phys.*, vol. xxi.

Mollard, J. . . . Les Nerfs du Cœur. *Rev. gén. d. Histol.*, vol. ix., 1908.

Möllendorf, W. . . Ueber abnorme Erhaltung der Sinusklappen im rechten Vorhof eines menschlichen Herzens. *Anat. Anz.*, Bd. 40.

Mollier, J. . . . In Hertwig's Handbuch der Entwicklungslehre, Bd. 1, 1906.

Mönckeberg, J. G. . Der normale histologische Bau und die Skelerose der Aortenklappen. *Virchow's Arch.*, Bd. 176.

,, . . Ueber die sogenannten abnormen Sehenfäden im linken Ventrikel des menschlichen Herzens und ihre Beziehungen zum Atrioventrikularbündel. *Verh. d. Deutsch. Path. Ges.*, 12 Tagung, Kiel, 1908.

,, . . Zur Frage der besonderen muskulären Verbindung zwischen Sinus und Atrioventrikularknoten im Herzen. *Zentralbl. f. Herzkrankh.*, 1910.

,, . . Untersuchungen übei das Atrioventrikularbündel im Menschlichen Herzen. Jena, 1908.

,, . . Herzmissbildungen mit besonderer Berücksichtigung des Atrioventricular Systems. 1922.

,, . . Die Erkrankungen des Myokards und des specifischen Muskelssystem. Henke u. Lubarsch, *Handb. d. spez. path. Anat. u. Hist.*, 1924.

Monrad-Krohn, G. H. . Le faisceau atrio-ventriculaire dans le cœur humain. *Arch. du Mal. du Cœur.*, T. 4, 1911.

Morison, A. . . . On the Innervation of the Sino-auricular Node (Keith-Flack) and the Auriculo-ventricular Bundle (Kent-His). *Jour. Anat. and Phys.*, vol. xlvi., 1910.

,, . . The Auriculo-ventricular Node in a Malformed Heart. *Ibid.*, vol. xlvii., 1911.

Mouchet, A. . . Vaisseaux lymphatiques du cœur chez l'homme et les mammiféres. *Compt. Rend. Soc. Biol.*, T. 66, 1909, No. 6.

,, . . Les vaisseaux lymphatiques du cœur chez l'homme et quelque mammiféres. *Jour. de l'Anat. et de la Physiol.*, Année 45, No. 5.

,, . . L'artère du pilier antérieur du ventricule droit. *Comp. rend. de l'Assoc. des Anat.*, 1926.

Müller u. Jaschke . Zür Frage der Herzgrösse am Ende der Schwangerschaft. *Munch. med. Wochensch.*, 1911.

Nagayo, M. . . . Zur normalen und pathologischen Histologie des Endocardium parietale. *Beitr. z. path. Anat. u. allg. Path.*, Bd. 45.

Nicoli, J. . . . Beiträge zur Anatomie und Physiologie des Salpenherzens. *Arch. f. Anat. u. Phys.*, Abt., 1908, Suppl.

Nussbaum, A. . . Ueber das Gefässsystem des Herzens. *Arch. f. mikrosk. Anat.*, Bd. 80, No. 3, 1912.

Odinzow, M. . . . Vascularisation der Herzklappen im Kindesalter. Inaug. Diss., München, 1904.

Ollendorff, A. . . Zur Frage der glatten Muskelfasern in dei Intima der Aorta. *Anat. Anz.*, Bd. 38.

Openchowsky, S. . . Beitrag zur Kenntnis der Nervenendigung im Herzen. *Arch. f. mikrosk. Anat.*, Bd. 22.

Oppenheimer, A. and B. S. . . The Relation of the Sino-auricular Node to the Venous Valves in the Human Heart. *Anat. Record*, vol. vi., 1910.

,, ,, .. The Innervation of Nodal Tissue. *Jour. Exp. Med.*, 1912, No. 2.

Ott, W. . . . Zur Kenntnis der Ganglienzellen des menschlichen Herzens. *Prager med. Wochenschr.*, 1886, No. 20.

Pace, D. . . . Ricerche sul tessuto nodale sopraventricolare del cuore. *Atti R. Accad. med. chir. di Napoli*, 1911.

Pagenstecher, W. . . Weiterer Beitrag zur Herzchirurgie. Die Unterbindung der verletzten Arteria coronaria. *Deutsche med. Wochenschr.*, 1901

Paladino, G. . . Per una questione di priorità. *Rend. della R. Accad. delle Sc. di Nat. Sc.*, 1909.

" . . Ancora per una questione di priorità a proposito del fascio atrio-ventricolare del cuore. *Anat. Anz.*, Bd. 46, 1914.

Pankul, E. . . Die physiologische Bedeutung des Hisschen Bündels. *Zeitschr. f. Biol.*, Bd. 51, 1908.

" . . Le faisceau atrio-ventriculaire de His. *Compt. Rend. Soc. Biol.*, T. 64, No. 24.

Papez, J. . . Musculature of the Atria. *Amer. Jour. Anat.*, vol. xxvii., 1919.

Papillian, V. . . Der Zusammenhang des sinus venosus mit der vena cava sinistra. *Anat. Anz.*, Bd. 57, 1923.

Parrot, J. . . Sur les hémato-nodules cardiaques chez les jeunes enfants. *Arch. d. Physiol. norm. et pathol.*, 1874.

Patten, C. J. . . On the Configuration of the Heart in Man and some other Mammals. *Jour. Anat.*, vol. xxxv., 1901.

Peacock, T. B. . . Malformations of the Heart. 1866 (2nd Ed.), London.

" . . On the Weight and Dimensions of the Heart in Health and Disease. *Monthly Jour.*, Sept. 1854.

Perman, E. . . Anatomische Untersuchungen über die Herznerven. *Zeitschr. f. d. gesam. Anat.*, Abt. 1, Bd. 71, 1924.

Pettigrew, J. B. . . On the Structure and Function of the Valves of the Vascular System in Vertebrata. *Proc. Roy. Soc. Edin.*, vol. xxiii., 1866.

" . . On the Arrangement of the Muscle Fibres in the Ventricles of the Vertebrate Heart. *Phil. Trans. Roy. Soc.*, 104, 1864.

Piquand, G. . . Recherches sur l'anatomie des vaisseaux sanguins du cœur. *Jour. de l'Anat. et Physiol.*, T. 46, 1910.

Pocharissky, J. F. . . Ueber zwei seltene Anomalien der Sehnenfäden im menschlichen Herzen. *Beitr. z. pathol. Anat.*, Bd. 35, 1905, Heft 3.

Poirier, P. . . Leçons sur le développement du cœur. *Gaz. des Hôpitaux*, Année 86, 1902-3, No. 125.

Pohlman, A. G. . . The Course of the Blood through the Heart of the Fœtal Mammal. *Anat. Record*, vol. iii., 1909.

Potain, J. . . De la mensuration du cœur par la radiographie; comparaison des deux méthodes. *La Semaine méd.*, 1901.

Rainer, F. J. . . Contribution à l'étude des lymphatiques superficiels du cœur. *Compt. Rend. Soc. Biol.*, T. 65, 1908.

" . . Le systéme lymphatique du cœur. Etude d'anatomie comparée. *Ann. Biol.*, T. 1, Paris, 1911.

" . . Ueber das Vorkommen von subepicardielen Lymphdrüsen beim Menschen. *Anat. Anz.*, Bd. 31, 1907.

Reichert, C. . . Angaben über Purkinjesche Fäden. *Müller's Arch.*, 1855.

Renaut, J., et Mollard, J. . . Le myocarde. *Revue gén. d'Hist.*, T. 1, 1905.

Retterer et Lelievre . Structure du myocarde de quelques vertébrés inférieurs. *Compt. Rend. Soc. Biol.*, T. 66 et T. 72.

Retzer, K. . . Ueber die muskulose Verbindung zwischen Vorhof und Ventrikel des Säugetierherzens. *Arch. f. Anat. u. Phys.*, Anat. Abt., 1904.

" . . The Atrio-ventricular Bundle and Purkinje-fibres. *Amer. Jour. of Anat.*, vol. vi., 1903.

" . . Some Results of Recent Investigation on the Mammalian Heart. *Anat. Record*, vol. ii., 1902.

" . . The Sino-ventricular Bundle. Cont. to *Embry.*, No. 272. Carnegie Instit., Washington, 1920.

Retzius, G. . . Biologische Untersuchungen. *N.F. Hefte*, 3.

Robertson, Jane . . Development of Heart of Lepidosiren. *Quart. Jour. Med. Sc.*, vol. lix., 1913.

Robinson, A. . . The Early Stages of the Development of the Pericardium. *Jour. Anat. and Phys.*, vol. xxxvii., 1902.

Rokitansky . . Handbuch der pathologischen Anatomie. Die Defecte der Scheidewände des Herzens. Wien, 1875.

Röse, C. . . . Beiträge zur vergleichenden Anatomie des Herzens der Wirbeltiere. *Morphol. Jahr.*, Bd. 16.

,, . . . Beiträge zur Entwicklungsgeschichte des Herzens. Heidelberg, 1888.

Rouviere. H. . . Développement du sinus transverse du pérecarde chez lapin. *Bib. anat.*, T. 13, Fasc. 3.

,, . . Des connexions du péricarde avec le diaphragme. *Compt. Rend. d. l'Assoc. d'Anat.*, Liege, 1903.

,, . . Étude sur le développement du péricarde chez le lapin. *Jour. de l'Anat. et Physiol.*, Année 40, No. 6.

Schafer, E. A. . . Les vaisseaux coronaires ont-ils des nerfs vasomoteurs. *Arch. des Soc. biol. p. p. l'Inst. Imp. de Méd. expér. á St Pétersbourg*, T 11, Suppl., 1904.

Schonberg, M. . . Ueber Veränderung im Sinusgebiet bei chronischer Arrhythmie. *Frankf. Zeitschr. f. Path.*, 1909.

,, . . Weitere Untersuchungen des Herzens bei chronischer Arrhythmie. *Frankf. Zeitschr. f. Path.*, 1909.

Schumacher, S. v. . Zur Frage der Herzinnervation bei den Säugetieren. *Anat. Anz.*, Bd. 21, 1902.

,, . . Die Herznerven der Säugetiere und des Menschen. *Sitzungber. d. k. k. Akad. d. Wiss. Wien*, 1902.

Schwalbe, E. . . Die Morphologie der Missbildungen der Menschen. Jena, 1906.

Schwartz, G. . . Ueber die Lage der Ganglienzellen im Herze der Säugetiere. *Arch. f. mikr. Anat. u. Entwickl.*, Bd. 53, 1910.

Seipp, L. . . . Das elastiche Gewebe des Herzens. *Anat. Hefte*, Bd. 6, 1896.

Shaner, R. F. . . On the Muscular Architecture of the Vertebrate Ventricle. *Jour. Anat.*, vol. lviii., 1923.

Smirnow, A. E. v. . Zur Frage von der Endingung der motorischen Nerven in den Herzmuskeln der Wirbeltiere. *Anat. Anz.*, Bd. 18, 1900.

,, . Einige Bemerkungen über die Existenz von Ganglienzellen in den Herzventrikeln des Menschen und einiger Säugetiere. *Anat. Hefte*, Bd. 27.

Spalteholz, W. . . Ueber Arterien der Herzwand. *Verh. d. Deutsch. Pathol. Ges.*, 13 Tag, Leipzig, 1909.

,, . . Die Coronararterien des Herzens. *Verh. Anat. Ges.*, 21 Vers, Würzburg, 1907.

,, . . Zur vergl. Anatomie der Arteriae coronariae cordis. *Verh. d. Anat. Ges.*, 22 Vers, Berlin, 1908.

,, . . Die Arterien der Herzwand. Leipzig, 1924.

Spalteholz und Hirsch, C. . Coronarkreislauf und Herzmuskel, anatomische und experimentelle Untersuchungen. *Verh. d.* 24 *Kongr. f. inn. Med.*, Wiesbaden, 1907.

Stieda, L. . . . Ueber quergestreifte Muskelfasern in der Wand der Lungenvenen. *Arch. f. mikr. Anat.*, Bd. 14.

Tanasescu, K. . . Sur la topographie des vaisseaux lymphatique du cœur. *Bibliographie anat.*, T. 17, 1908.

Tandler, J. . . . Die Entwicklungsgeschichte des Herzens, in Keibel-Mall's *Handbuch der Entwicklungsgeschichte des Menschen*, Leipzig, 1911.

,, . . . Anatomie des Herzens. 1913.

Tawara, K. . . . Ueber die sogenannten abnormen Sehnenfäden des Herzens. *Ziegler's Beiträge*, Bd. 39, 1906.

,, . . . Das Reisleitungssystem des Säugetiereherzens. Jena, 1906.

Théremin, J. . . Études sur les affections congenitales du cœur. Paris, 1895.

Thomson, P. . . Some notes on the Development of the Heart. *Brit. Med. Jour.*, 1909.

Thorel, C. . . . Vorläufige Mitteilungen über eine besondere Muskelverbindung zwischen der Cava superior und dem Hisschen Bündel. *Münch. med. Wochenschr.*, Jahr. 56, No. 42.

,, . . . Ueber den Aufbau des Sinusknotens und seins Verbindung mit der Cava superior und den Wenkebachschen Bündeln. *Münch. med. Wochenschr.*, No. 4, 1910.

Thorel, C. . . . Über die supraventrikularen Abschnitte des sogenannten Reizleitungssystem. *Verh. der. D. Path. Ges.*, 1910.

Tufts, J. M. . . Observations on the Structure of the Purkinje Fibres. *Anat. Record*, vol. xxii., 1922.

Ungar, M. . . Das specifischen System der menschlichen Herzen. Lotus. Prague, 1924.

Veraguth, O. . . Untersuchungen uber normale und entzundete Herzklappen. *Arch. f. path. Anat.*, Bd. 139.

Vermes, E. . . Ein Beitrag zur vergleichenden Anatomie des Reizleitungssystem des Säugetierherzens. *Anat. Anz.*, Bd. 60, 1926.

Vischia, Q . . Beitrag zum Studium der Arteriae coronariae cordis. *Anat. Anz.*, Bd. 61, 1926.

Wang, W. . . . Development of Heart (Ferret). *Jour. Anat.*, vol. lii., 1917.

Waterson, D. . . Development of the Heart in Man. *Trans. Roy. Soc. Edin.*, vol. lii., Part II., 1918.

" . . Developmental Changes in the Pericardium. *Jour. Anat.*, vol. l., 1915.

Weber, A. . . . Formation réticulée de l'oreillette droite. *Bibl. anat.*, T. 6, 1898.

" . . . Restes de la valvule veineuse. *Bibl. anat.*, T. 13.

" . . . Recherches sur quelques etudes du developpement du cœur de la Race. *Compt. Rend.*, 1908.

Wegelin, C. . . Ueber die Blutknötchen an den Herzklappen der Neugeborenen. *Frankf. Zeitschr. f. Pathol.*, 1899.

Wenckebach, K. F. . Beiträge zur Kenntnis der menschlichen Herztätigheit. *Arch. f. Anat. u. Phys.*, Phys. Abt., 1906-7.

Wiedersheim, R. . Grundriss der vergleichenden Anatomie, 1902.

Wilson, J. G. . . Is the Atrio-ventricular Bundle to be Regarded as a Neuro-muscular Spindle ? *Anat. Record*, vol. iii., No. 4, 1909.

" . . . Nerves of the Atrio-ventricular Bundle. *Proc. Roy. Soc. London*, Ser. B., Biol. Ser., vol. lxxxi., No. 546.

" . . . The Nerves of the Atrio-ventricular Bundle. *Anat. Record*, vol. iii., No. 4, 1909.

de Witt, Lydia . . Observations on the Sino-ventricular Connecting System of the Mammalian Heart. *Anat. Record*, vol. iii., No. 4, 1909.

Woollard, H. H. . The Innervation of the Heart. *Jour. Anat.*, vol. lx., 1926.

Yoshinaga, T. . . The Early Development of the Heart in Mammalia. *Anat. Record*, vol. xxi., 1921.

Zimmermann, W. . Das Reisleitungssystem des Herzens bei Equidae. *Anat. Anz.*, Bd. 57, 1923.

INDEX

Printed in Great Britain by The Darien Press, Edinburgh